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# Growth performance and metabolic changes in lambs and steers after mild nutritional restriction

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## SUMMARY

Two trials investigating compensatory growth are reported in which lambs and young cattle were placed on either a continuous (C) or a discontinuous (RR) growth path. RR animals were subjected to a phase of restricted feeding and then realimented at an equivalent level of feeding to C animals over the same live-weight range. Eight 4-month-old lambs and 30 9-month-old Swiss Brown steers were used. The restriction (I) and realimentation (II) phase covered the live-weight ranges 23–32 kg and 32–44 kg respectively in the lamb trial and 236–310 kg and 310–460 kg respectively in the steer trial.

Fifty-six total energy balances were made with lambs using open-circuit respiration calorimetry. Fifty determinations of diet digestibility and N balance were made with steers. Lambs received a pelleted concentrate diet and, except for restrictively fed steers which received hay alone, steers were offered a diet based on maize silage. The restriction phase of RR lambs and RR steers was longer, and the daily ME intake and daily live-weight gains were significantly lower than those of the C animals.

Compared with C lambs a marked reduction in methane production of RR lambs occurred during feed restriction which persisted throughout realimentation.

During recovery realimented lambs gained non-significantly, but realimented steers significantly, more than C animals from a similar ME intake and required less ME/kg daily live-weight gain. Realimented lambs retained more protein at the start of recovery compared with C lambs but both C and realimented steers retained similar amounts of nitrogen. Indirect evidence is presented that suggests improved utilization of ME for protein deposition, at least at the start of realimentation.

Although the animals on the discontinuous growth path (RR) took longer to reach slaughter weight, their total intake of gross energy and overall energy conversion ratio (MJ ME/kg live-weight gain) was similar to those of animals on the continuous growth path (C).

## INTRODUCTION

The ability of animals to express compensatory growth following a period of nutritional limitation is well documented (Wilson & Osbourn, 1960; Allden, 1970). Little doubt remains that increased appetite, and the associated gut-fill effect, is an important factor responsible for compensatory growth. However, disagreement remains concerning the causal involvement of the following three factors in the complex of changes resulting in compensatory growth. First, a reduction of maintenance requirement; second, a fall in the energy value of the body-weight gains and third, an increased efficiency of feed utilization. The close interdependency between these three factors, together with level of feeding differences, and their individual effects on efficiency (Bickel, 1977), often makes it difficult to interpret the results of studies on compensatory growth. For example, the frequently but not universally observed higher feed intake of compensating animals (Allden, 1970) prevents the separation of the effects on growth rate of the higher feeding level from any increased efficiency or decreases in the energy value of the gains associated with compensatory growth.

In 1975 a research programme was initiated at

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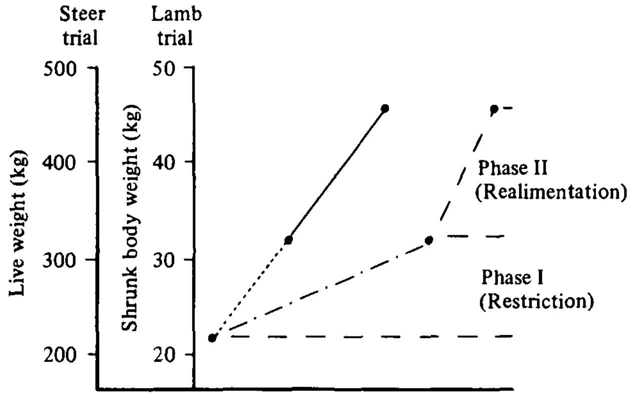


Fig. 1. Experimental plan of lamb and steer trial. - - - - -, $C_I$ lambs and steers; ———, $C_{II}$ lambs and steers; —·—, $RR_I$ lambs and steers; – – –, $RR_{II}$ lambs and steers; ●, slaughter groups of six steers.

Zürich with the objective of re-examining the role of the four factors in the compensatory growth complex. There was, furthermore, a need to investigate the performance of cattle in a semi-intensive fattening system designed to maximize the input of home-grown feedingstuffs. Such a system can involve a store period (Lörtscher, Weber & Zaugg, 1975) when cattle graze summer alpine pasture and compensate in winter when offered diets based on maize silage. In other regions cattle compensate when fed cereal-based diets during early winter following restricted growth on autumn pasture or compensate on early summer pasture following a late winter phase which enables the input of low to medium quality conserved forages.

This paper describes a metabolism trial with lambs and a growth trial with steers in which compensating animals were given the same feed allowance over the same live-weight interval as control animals on a continuous growth path. Such a design avoids the confounding influence of differences in level of feeding and maintenance requirements on growth performance and energy conversion ratio (MJ ME per kg live-weight gain). Respiration and slaughter trials with cattle designed to examine in more detail the interactions between the various factors in the compensatory growth complex will be reported subsequently. A comprehensive description of the trials is given elsewhere (Thomson, 1979).

## MATERIALS AND METHODS

### *Experimental plan*

The plan of the lamb and the steer trial is shown in Fig. 1. Each trial involved a control (C) and a restricted–realimented (RR) group. C lambs and C steers were fed during 120 and 266 days respectively to allow continuous growth. RR lambs and RR steers were subjected to a 144- and 154-day period of mild feed restriction (phase I) respectively followed by realimentation (phase II) of 56 and 147 days respectively at the same level of feeding as C lambs and C steers.

Comparisons of performance of corresponding groups during the restriction ($C_I$ *v.* $RR_I$) and realimentation phase ($C_{II}$ *v.* $RR_{II}$ animals) were made over the same live-weight interval.

*Animals.* The number of animals in the respective groups of the two trials and the level of feeding are shown in Table 1. Eight 4-month-old Swiss White Alpine lambs were divided between groups C and

Table 1. *Number of animals, level of feeding and target daily gains of respective groups*

| | | Restriction phase | | Realimentation phase | |
|---|---|---|---|---|---|
| | | $C_I$ | $RR_I$ | $C_{II}$ | $RR_{II}$ |
| Number of animals | Lambs | 4 | 4 | 3 | 4 |
| | Steers† | 12‡ | 12‡ | 6 | 6 |
| Level of feeding* | Lambs | 1·7 | 1·4 | 2·7 | 2·7 |
| | Steers | 2·3 | 1·4 | 1·7 | 1·7 |
| Target daily gains (g) | Lambs | 208 | 50 | 250 | 250 |
| | Steers | 880 | 310 | 880 | 880 |

† Six additional steers comprised initial slaughter group.

‡ Six of these steers slaughtered at end of restriction phase.

* Expresses ME intake as multiples of ME requirement for maintenance.

Table 2. *Proximate composition of the diets*

| | Lamb trial | | Steer trial | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Phase... | I | II | I | | | II | | | |
| Component... | Pellets | Pellets | Hay | Maize silage | Concentrate | Maize silage | Maize silage | Concentrate | Concentrate |
| Dry matter (D.M.) | 90·5 | 90·6 | 85·5 | 36·4 | 88·2 | 23·9 | 36·6 | 89·9 | 88·0 |
| Ash (% in D.M.) | 6·6 | 6·0 | 9·9 | 3·9 | 9·4 | 4·6 | 5·1 | 15·1 | 6·7 |
| Crude protein (% in D.M.) | 15·1 | 14·2 | 8·6 | 9·0 | 23·8 | 9·0 | 8·3 | 45·3 | 16·0 |
| Gross energy (MJ/kg D.M.) | 17·8 | 17·9 | 18·4 | 18·4 | 17·6 | 19·4 | 18·3 | 17·5 | 17·7 |

RR. They were treated against gut parasites and accustomed to the ration for 4 weeks before the trial started.

Initially 30 9-month-old Swiss Brown steers were available at the beginning of the steer trial which was based on a comparative slaughter design. Six representative steers formed an initial group and thereafter six steers from the group C and RR were slaughtered at the end of the restriction and realimentation phase. Thus in the steer trial groups $C_I$ and $RR_I$ involved 12 animals each and group $C_{II}$ and $RR_{II}$ six animals each.

*Estimation of feed requirements.* The Agricultural Research Council (1965) conventions were used to formulate the feed allowances for the lambs. The target daily shrunk body-weight gain of the lambs is given in Table 1. The steers were fed diets estimated from Ministry of Agriculture, Fisheries and Food (1975) allowances to sustain target daily live-weight gains (LWG) given in Table 1. In doing so it was appreciated that the estimated energy values of the gain used by the Ministry of Agriculture, Fisheries and Food (1975) were based on limited data which gives a further approximation when applied to the dual purpose, late-maturing Swiss Brown breed. The energy value of the steers diets (ME/D.M.) were estimated by multiplying the content of digestible energy by 0·82 (Agricultural Research Council, 1965).

The amount of diets fed in both trials was adjusted every 14 days according to a predetermined target growth schedule based on the LWG and the estimated empty-body weights at the start of the two growth phases. No correction to feed allowances were made when actual LWG deviated from the target growth schedule.

*Diets.* The proximate composition of the diets are given in Table 2.

Lambs were offered a pelleted cereal diet containing 20 % chopped straw, 5 % molasses, 55 % rolled wheat, 8 % extracted soya-bean meal and a vitamin–mineral premix in the restriction phase. In the realimentation phase the straw and soya-bean meal were reduced to 10 and 5 % respectively, and the wheat increased to 78 %. Diets I and II contained 11·7 and 12·6 MJ ME/kg D.M. respectively.

Apart from the $RR_I$ steers which received hay alone, all the other groups of steers were offered a diet based on maize silage balanced with appropriate protein concentrate and vitamin–mineral premixes.

*Procedures*

*Housing and feeding.* Lambs were penned on sawdust in a controlled environment house and steers tethered in a cowshed fitted with a wooden slatted floor. Lambs were fed at 09.00 and steers at 08.00 and 16.00 h. Daily feed intake of individual animals was recorded throughout the trials.

*Measurement of heat production.* Heat production of lambs was estimated from gaseous exchange (Brouwer, 1965) measured with open-circuit respiration equipment (Daccord, 1970; Wenk, Prabucki & Schürch, 1970). Oxygen, $CO_2$ and $CH_4$ concentrations were determined using a Taylor Servomex (Type AO 184) analyser, a Siemens Ultramat M and a Siemens Ultramat 2 respectively. Heat production was measured four times on each C lamb and ten times on each RR lamb. Each measurement consisted of four consecutive 24 h determinations except the last 48 h of 9-day period of maintenance feeding and over the final 48 h of a subsequent 5-day period of fasting.

*Digestibility and nitrogen balance.* Excreta collections lasted 9 and 7 days in the lamb and steer trial respectively. Lambs were transferred in their metabolism crates to the respiration chambers for the last 4 days of each collection period. Four steers from each experimental group were placed in metabolism crates to make a total of 50 determinations of digestibility and nitrogen balance.

*Chemical analyses.* Samples of feed and excreta were analysed for proximate components by Weende procedures, for gross energy by bomb calorimetry and for carbon as described by

Table 3. *Digestibility, metabolizability and content of metabolizable energy in the digestible energy (ME/DE)*

| | | Restriction phase | | | Realimentation phase | | |
|---|---|---|---|---|---|---|---|
| | | $C_I$ | $RR_I$ | S.E. of the difference | $C_{II}$ | $RR_{II}$ | S.E. of the difference |
| Digestibilities (%) | | | | | | | |
| Dry matter | Lambs | 71·7 | 74·4 | 1·35 | 77·4 | 78·2 | 1·37 |
| | Steers | 73·0 | 70·7 | — | 77·2 | 68·5* | 1·23 |
| Gross energy | Lambs | 69·7 | 73·0 | 1·82 | 77·0 | 76·7 | 1·49 |
| | Steers | 71·4 | 69·0 | — | 70·9 | 66·9* | 1·21 |
| Crude protein | Lambs | 68·6 | 72·1* | 1·42 | 72·0 | 72·1 | 2·04 |
| | Steers | 66·2 | 66·3 | — | 63·2 | 59·7 | 1·74 |
| Metabolizability (%) | Lambs | 60·1 | 63·0 | 1·68 | 68·2 | 71·1 | 1·21 |
| ME/DE (%) | Lambs | 87·5 | 86·3 | — | 88·3 | 92·6* | 1·00 |

* Significantly different from the control group ($P < 0{\cdot}05$).

Schneider (1959). Urinary energy was estimated from urinary carbon (Blaxter, Clapperton & Martin, 1966).

*Body weights.* Lambs were weighed on entering and leaving the chambers 23 h after the last meal to give shrunk body weight (SBW). Apart from live-weight (W) determinations at the beginning and end of the two growth phases, all steers were weighed every 14 days at 15.00 h, about 8 h after their last meal.

*Slaughter procedures and carcass specific gravity.* At the beginning of the trial and at the end of phases I and II all steers were weighed at 05.30 h, about 13·5 h after the last meal. All were then given the morning meal, but not the afternoon meal. After the morning meal animals in the respective slaughter groups (Fig. 1) were transported for about 90 min to a commercial abattoir. These animals, and those remaining on trial, were then weighed again about 26 h after the last meal to give shrunk body weight (SBW). Water was not available during the 26 h interval.

Immediately after the SBW determination, slaughter of respective steers took place by captive bolt. The intact alimentary canal, urinary and gall bladder was removed, weighed, emptied of all contents, rinsed out, allowed to drain and re-weighed. The weight loss represented gut contents. Empty body weight was calculated from SBW minus gut contents.

The carcasses were weighed warm to give carcass weight and stored at 4 °C for 48 h. After halving down the centre of the vertebral column, one side was quartered between the 11th and 12th ribs, and the quarters weighed in air using commercial equipment to the nearest 100 g. Quarters were then immersed in water at 4 °C and re-weighed to the nearest 100 g. Carcass specific gravity was determined as described by Lofgreen (1965), and carcass energy content from relationships between carcass specific gravity, body water and fat (Garrett & Hinmann, 1969).

*Experimental problems.* Because lambs often refused feed when in the respiration chambers, 11 of the 56 energy balances were discarded from the analysis since refusals exceeded 20 % of total feed offered over the 4 days in the chambers. One C lamb continuously refused significant amounts of feed and its data were excluded from the analysis. However, at least three successful balances on each of the remaining seven lambs were made during phase II.

No intake or health problems were encountered in the steer trial.

Owing to technical difficulties during determination of specific gravity at the abattoir, the specific gravity values of $RR_I$ steers had to be discarded.

*Statistical analysis.* The linear regression of live weight on time of the individual animals gave the best fit for estimating LWG within phases I and II. The intakes and performance of the group $C_I$ *v.* $RR_I$, $C_{II}$ *v.* $RR_{II}$ and $C_{I+II}$ *v.* $RR_{I+II}$ were compared using Student's *t* test (Snedecor & Cochran, 1967). Since there was a close relationship between digestibility and SBW in the lamb trial (Thomson, 1979), means of variables affected by this relationship, e.g. digestibility and metabolizability, have been adjusted to a common SBW of 38 kg during phase II by linear interpolation.

## RESULTS

*Digestibility and metabolizability.* The digestibility, metabolizability and the ratio metabolizable

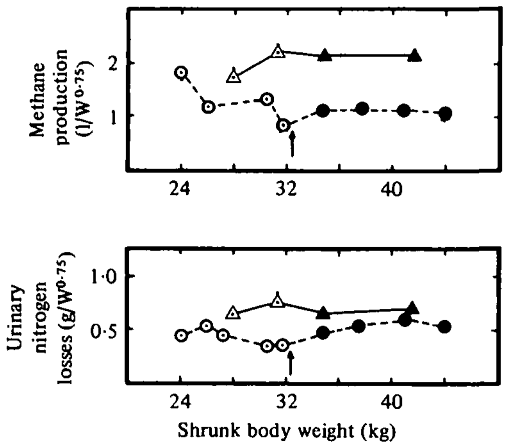


Fig. 2. Daily methane production and urinary losses of lambs. △, $C_I$; ▲, $C_{II}$; ⊙, $RR_I$; ● $RR_{II}$; ↑, start of realimentation.

Table 4. *Digestibility of the diet offered to steers during realimentation*

| Period | Live weight (range, kg) | $C_{II}$ | $RR_{II}$ | S.E. of the difference |
|---|---|---|---|---|
| 1 | 300–369 | 72·4 | 66·7** | 1·27 |
| 2 | 365–405 | 70·3 | 63·6* | 1·84 |
| 3 | 382–449 | 69·8 | 69·0 | 3·16 |
| 4 | 409–469 | 70·9 | 68·3 | 1·06 |

* Significantly different from the control group ($P < 0·05$).

** Significantly different from the control group $P < 0·01$).

energy to digestible energy (ME/DE) of the diets are shown in Table 3. An improvement in the digestibility of the diets occurred as the lamb trial progressed. This was due to a live-weight effect rather than to a level of feeding effect or to slight change in the composition of the diet.

Methane and urinary nitrogen losses were low throughout the lamb trial. Thus metabolizable energy (ME) content of the pelleted diet was between 86·3 and 92·6 % of digestible energy (DE) (Table 3). Feeding the same diet to rehabilitating adult sheep, Gingins (1978) found similar results. These values are well above the generalized value of 82 % recommended by the Agricultural Research Council (1965). Methane production of lambs declined during restricted feed intake and remained at a lower level ($P < 0·05$) during realimentation than in control lambs. Urinary nitrogen losses also declined somewhat but increased again during realimentation (Fig. 2). Thus the significant ($P < 0·05$) difference in the ME/DE ratio between the two groups during phase II (Table 3) was mainly due to differences in methane production.

In the steers trial digestibility was the same for both groups in phase I (Table 3). During realimentation digestibility of the dry matter and energy, but not of protein, was significantly lower when determined on $RR_{II}$ compared with control steers. This was due to the low digestibility of the diet during the first two periods of realimentation (Table 4).

*Intakes.* The restriction of feed intake during phase I was more severe in the lamb trial than in the steer trial (Table 5). During phase II scaled intake (expressed per metabolic weight) of control and realimented lambs was similar. However, scaled D.M. intake of realimented steers was lower than that of control animals. This, together with the lower digestibility of energy (Table 3), reduced their overall scaled ME intake to 92 % of that of $C_{II}$ steers.

The scaled D.M. intake of both $C_{II}$ and $RR_{II}$ lambs was under 80 g D.M./$W^{0·75}$ and therefore appetite limitations are not held responsible for the refusals when lambs were in the chambers. Similar problems were encountered by Graham & Searle (1975) and highlight difficulties of quantifying *ad libitum* intake of lambs confined to respiration chambers.

*Nitrogen, protein and fat retention.* Retained nitrogen per kg metabolic weight was similar for control lambs throughout the experiments (Table 6). Nutritionally restricted lambs showed lower, realimented lambs higher nitrogen retention than control lambs, although the latter difference was not statistically significant ($P > 0·05$). However, by analysing the different periods of phase II a considerably higher protein deposition at the start of realimentation was identified (Table 7).

The changes in protein and fat retention in relation to ME intake are shown in Fig. 3. The $RR_I$ lambs were retaining protein at the expense of body fat, which remained in negative balance during the restriction phase. There was a close parallel between fat retention and ME intake throughout the trial. Fat retention of $RR_{II}$ lambs reached high levels after only 14 days realimentation.

The protein supplied to steers was reduced during the realimentation compared with the restriction phase in order to avoid non-specific use of dietary protein and excess urinary nitrogen losses (Table 8). Retained nitrogen was slightly, although not significantly ($P > 0·05$), lower in $RR_{II}$ steers compared with $C_{II}$ steers.

*Partial efficiency of utilization of ME.* In order to

Table 5. *Scaled daily intake of dry matter, metabolizable energy and daily intake of crude protein*

| | Restriction phase | | | Realimentation phase | | |
|---|---|---|---|---|---|---|
| Daily intake of: | $C_I$ | $RR_I$ | S.E. of the difference | $C_{II}$ | $RR_{II}$ | S.E. of the difference |
| Dry matter ($g/W^{0.75}$) | | | | | | |
| Lambs | 77·9 | 44·9*** | 2·2 | 78·3 | 74·8 | 3·7 |
| Steers | 69·6 | 60·5*** | 0·67 | 72·6 | 70·6* | 0·87 |
| Metabolizable energy ($kJ/W^{0.75}$) | | | | | | |
| Lambs | 873 | 504*** | 17·5 | 945 | 955 | 43·5 |
| Steers† | 734 | 621 | — | 765 | 701 | — |
| Crude protein (g) | | | | | | |
| Lambs | 139 | 79*** | 6·0 | 166 | 163 | 3·8 |
| Steers | 620 | 640** | 0·6 | 690 | 670* | 1·1 |

† Estimation from intake of digestible energy multiplied by 0·82.
* Significantly different from control group ($P < 0.05$).
** Significantly different from control group ($P < 0.01$).
*** Significantly different from control group ($P < 0.001$).

Table 6. *Nitrogen intake, losses and retention and fat retention in the lambs as measured during determinations of energy balance*

| | Restriction phase | | | Realimentation phase | | |
|---|---|---|---|---|---|---|
| | $C_I$ | $RR_I$ | S.E. of the difference | $C_{II}$ | $RR_{II}$ | S.E. of the difference |
| Nitrogen intake ($g/W^{0.75}$) | 1·77 | 1·07*** | 0·076 | 1·79 | 1·68 | 0·079 |
| Faecal nitrogen ($g/W^{0.75}$) | 0·56 | 0·30*** | 0·036 | 0·51 | 0·47 | 0·041 |
| Urinary nitrogen ($g/W^{0.75}$) | 0·63 | 0·42 | 0·088 | 0·70 | 0·54 | 0·048 |
| Retained nitrogen ($g/W^{0.75}$) | 0·59 | 0·35 | 0·087 | 0·57 | 0·68 | 0·098 |
| Fat retention ($g/W^{0.75}$) | 3·3 | −0·4 | 0·76 | 6·9 | 6·1 | 0·53 |

*** Significantly different from control group ($P < 0.001$).

detect possible differences in the utilization of ME between control and realimented lambs, partial efficiencies were estimated using regression procedures. The linear regression scaled retained energy ($RE/W^{0.75}$) on scaled ME intake ($MEI/W^{0.75}$) provides an estimate of the partial efficiency for gain ($k_{pf}$) and the multiple regression scaled MEI on scaled energy retained as protein ($REP/W^{0.75}$) and fat ($REF/W^{0.75}$) allows estimation of the partial efficiency for protein ($k_p$) and for fat deposition ($k_f$) respectively. The data from C and $RP_{II}$ lambs were analysed separately. The results of the analysis are shown in Table 9. Comprehensive original data are presented elsewhere (Thomson, 1979).

The partial efficiency for maintenance ($k_m = 0.68$) was higher th.n for growth ($k_{pf} = 0.56$ and 0·59). $k_{pf}$ of the two groups (regression models 2 and 3) did not differ significantly ($P > 0.05$), although the regression coefficient $b_1$ in model 3 is marginally higher than in model 2. The regression coefficient $b_1$ in model 5 was lower than in model 4, suggesting that partial efficiency for protein deposition ($k_p$) was higher in realimented lambs ($RR_{II}$) than in control lambs (C). However, $b_2$ shows the opposite tendency. Separately analysing the different periods of phase II showed that the partial efficiency for growth ($k_{pf}$) of $RR_{II}$ lambs was higher at the beginning of realimentation than of $C_{II}$ lambs.

No direct estimate of efficiency of ME utilization was possible in the steer trial. However, estimation of maintenance energy requirement ($ME_m$) was made by regressing daily empty-body-weight gain on MEI. Subtracting the derived $ME_m$ from total ME intake and estimating carcass

Table 7. *Changes in daily protein and fat deposition and partial efficiency of ME utilization for growth during realimentation phase of the lamb trial*

| | Protein deposition ($kJ/W^{0.75}$) | | Fat deposition ($kJ/W^{0.75}$) | | Partial efficiency for growth ($k_{pf}$) | |
|---|---|---|---|---|---|---|
| Group... Period† | $C_{II}$ | $RR_{II}$ | $C_{II}$ | $RR_{II}$ | $C_{II}$ | $RR_{II}$ |
| 1 | 86 | 116 | 238 | 251 | 0·52 | 0·60 |
| 2 | 88 | 98 | 238 | 256 | 0·55 | 0·60 |
| 3 | 82 | 93 | 299 | 224 | 0·61 | 0·56 |
| 4 | — | 97 | — | 233 | — | 0·56 |

† 14 days interval between the periods.

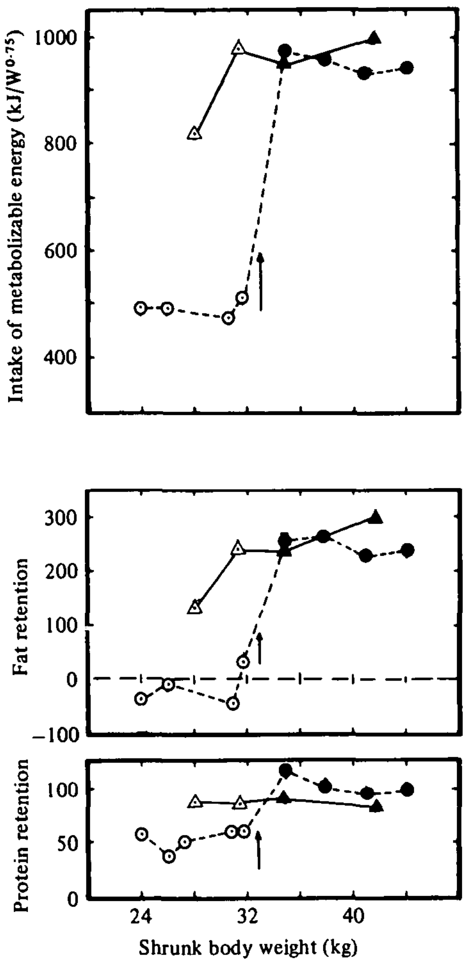


Fig. 3. Daily intake of metabolizable energy by lambs and retention of fat and protein. △, $C_I$; ▲, $C_{II}$; ⊙, $RR_I$; ●, $RR_{II}$; ↑, start of realimentation.

energy content from carcass specific gravity (Garrett & Hinman, 1969) allowed estimation of $k_{pf}$. The carcass specific gravity measurements from the initial and two final slaughter groups (Table 10) were used for the estimation of the carcass energy content of C and RR steers. The difference in the carcass energy content of the initial and final slaughter groups divided by the live weight gained over the complete trial gave an estimate of the energy value of body-weight gains ($EV_g$). An $ME_m$ of 462 $kJ/W^{0.75}$ was estimated, and, from an $EV_g$ of 10·5 and 9·8 MJ/kg live-weight gain for C and RR respectively, the $k_{pf}$ of the two groups was 0·36 and 0·43 respectively.

*Growth performance and energy conversion ratio.* The growth performance of $RR_I$ lambs and steers was highly significantly ($P < 0.001$) lower than controls (Table 11). Even though $RR_{II}$ lambs gained 4·6 kg more shrunk body weight than $C_{II}$ lambs during realimentation over a similar time interval, the difference did not reach significance ($P > 0.05$). The $RR_{II}$ steers exhibited significantly ($P < 0.05$) higher live-weight gain (LWG) than $C_{II}$ steers when realimented, but when expressed as empty-body-weight gain the difference did not reach significance ($P > 0.05$). However, during the 1st month of realimentation the LWG of $RR_{II}$ steers reached 1200 g.

Compensatory growth enabled $RR_{II}$ steers to improve significantly ($P < 0.01$) their energy conversion ratio compared with control animals. The difference in energy conversion ratio between $RR_{II}$ and $C_{II}$ lambs was not significant ($P > 0.05$).

*Gut fill and carcass characteristics.* The gut fill of $RR_I$ steers was significantly ($P < 0.05$) higher than that of $C_I$ steers because the basal diet consisted of hay instead of maize silage (Table 10). There were no differences in the killing-out percentages of the various groups although killing-out percentage increased as the steers became heavier.

No differences across steer groups in carcass specific gravity were noted.

Table 8. *Components of nitrogen balance in the steer trial*

| | Restriction phase | | | Realimentation phase | | |
|---|---|---|---|---|---|---|
| | $C_I$ | $RR_I$ | S.E. of the difference | $C_{II}$ | $RR_{II}$ | S.E. of the difference |
| ME intake† (kJ/$W^{0.75}$) | 718 | 640** | 16·5 | 762 | 688** | 13·0 |
| Nitrogen intake (g/$W^{0.75}$) | 1·45 | 1·55* | 0·024 | 1·27 | 1·21* | 0·014 |
| Faecal nitrogen (g/$W^{0.75}$) | 0·50 | 0·52 | 0·030 | 0·47 | 0·49 | 0·021 |
| Urinary nitrogen (g/$W^{0.75}$) | 0·45 | 0·66** | 0·056 | 0·41 | 0·39 | 0·049 |
| Retained nitrogen (g/$W^{0.75}$) | 0·50 | 0·37 | 0·060 | 0·39 | 0·33 | 0·036 |

† Values differ from those in Table 5 because only 4 of 6 animals used in balance trial.
* Significantly different from the control group ($P < 0{\cdot}05$).
** Significantly different from the control group ($P < 0{\cdot}01$).

*Overall performance.* The relatively long restriction period in the lamb trial considerably increased the total duration of the growth period of RR lambs (Table 12). However, the compensating steers reduced the 70-day interval between the groups at the start of realimentation to 35 days at slaughter. The milder degree compared with RR lambs resulted in only a 12 % increase in total fattening period. With regard to animals on the discontinuous growth path, RR steers required a similar amount of gross energy and RR lambs only 12 % more than the respective control groups on a continuous growth path. The overall energy conversion ratio of C and RR lambs was similar whereas RR steers required 6 % less ME per kg LWG than C steers.

## DISCUSSION

*Digestibility.* The depression of the digestibility of the fibrous maize-silage diet measured on the realimentated steers was not due to differences in dietary composition. In contrast to the steer trial no depression of digestibility was observed in the RR lambs offered a rapidly fermentable concentrate diet (Table 3). McManus, Reid & Donaldson (1972) and Drew & Reid (1975) also noted reduced digestibilities in compensating lambs but Asplund, Hedrick & Haugeback (1975) did not. The high digestibilities reported by Thornton *et al.* (1979) on the 1st day of realimentation appear to be due to applying the faecal output from the preceding period of near starvation feeding to the *ad libitum* intake on the 1st day of realimentation. Over the next 5 days digestibility decreased by over 20 percentage units.

In order to explain this unclear picture regarding an apparent digestibility depression at the beginning of realimentation, it is suggested that physiological changes take place in the animal which will affect digestibility only if the physical and chemical composition of the diets is appropriate. Physiological changes leading to an increase in the rate of passage would, in general, have little effect on the extent of digestion of a rapidly fermentable diet (lamb trial), but could affect a more fibrous diet (steer trial). Such an increase in the rate of passage in the compensating animal is an attractive proposition since it could be associated with the elevated appetite of these animals. However, it is suggested that any relationship between appetite and rate of passage may be mediated by triiodothyronine ($T_3$) since a positive association between $T_3$ and rate of passage (Miller *et al.* 1974; Kennedy, Young & Christopherson, 1977) and between $T_3$ and energy intake (Blum, Thomson & Bickel, 1979; Blum *et al.* 1980; Thomson *et al.* 1980) has been reported.

*Level of feeding and maintenance requirement.* Approximately the same scaled ME intake of $C_{II}$ and $RR_{II}$ animals was achieved during realimentation (Table 5). Thus, if it is assumed that the maintenance requirement ($ME_m$) of control and realimented animals was similar, then their level of feeding will have been almost equivalent. Except during the immediate post-restriction phase, this assumption is probably correct since it has been shown (Graham & Searle, 1975, 1979; Gingins, 1978) that $ME_m$ returns to near normal levels within the first few weeks of realimentation.

It is therefore considered that in these two trials, because there were no differences in the level of feeding between groups, this factor can be discounted when explaining the differences in energy conversion ratio between them.

*Partial efficiency of utilization of metabolizable energy.* The overall $k_{pf}$ of the control and realimentated lambs was similar (Table 9) which confirms the findings of Drew & Reid (1975) and Graham & Searle (1975, 1979) but not those of Meyer & Clawson (1964). But at the start of realimentation a small improvement in $k_{pf}$ was noted in both the lamb trial (Table 7) and in the

Table 9. *Estimates of partial efficiencies of utilization of ME for maintenance and growth of lambs*

| Regression model | $n$ | Group comparison | $Y$ | $b_o$ kJ/W$^{0.75}$ | $b_1$ (±S.E.) | $b_2$ (±S.E.) | R.S.D. kJ/W$^{0.75}$ | $r^2$ | $ME_m$† kJ/W$^{0.75}$ | $k_m$ | $k_p$ | $k_f$ | $k_{pf}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 18 | $RR_m+RR_f$ | NE* | −248·7 | 0·68 (0·036) | — | 18·8 | 0·98 | 364 | 0·68 | — | — | — |
| 2 | 14 | $C+RR_m$ | NE* | −210·1 | 0·56 (0·038) | — | 39·0 | 0·95 | 375 | — | — | — | 0·56 |
| 3 | 16 | $RR_{II}+RR_m$ | NE* | −218·6 | 0·59 (0·027) | — | 27·1 | 0·97 | 368 | — | — | — | 0·59 |
| 4 | 14 | $C+RR_m$ | MEI* | 368·9 | 3·06 (0·509) | 1·31 (0·170) | 57·6 | 0·96 | 369 | — | 0·33 | 0·75 | — |
| 5 | 16 | $RR_{II}+RR_m$ | MEI* | 373·1 | 2·06 (0·508) | 1·49 (0·193) | 45·4 | 0·97 | 373 | — | 0·49 | 0·67 | — |

Regression models 1, 2 and 3: NE* $= b_o + b_1$ MEI*.
Regression models 4 and 5: MEI* $= b_o + b_1$ REP* $+ b_2$ REF*.
* Scaled (W$^{0.75}$).
† ME requirement for maintenance, estimated from regression.
$RR_f$ Heat production measured on the 4th and 5th day of fast.
$RR_m$ Heat production measured at maintenance level of feeding.

study of Ørskov *et al.* (1976) with early weaned lambs.

Empirical models for estimating $k_p$ and $k_f$ suffer from auto-correlation between the independent variables. Therefore, it is hazardous to conclude directly from the results of the models 4 and 5 in Table 9, that the ME was utilized more efficiently for protein deposition by $RR_{II}$ lambs compared with $C_{II}$ lambs. However, an improved $k_p$ at the start of realimentation of lambs is suggested.

The estimated $k_{pf}$ in the steer trial (p. 189) indicated that steers during realimentation may be more efficient converters of ME than steers on a continuous growth path.

*Carcass characteristics and energy value of gain.* The design of the trials precluded the influence of gut fill on daily live-weight gain of realimented animals. The carcass specific gravity values (Table 10) showed little variation between slaughter groups and are similar to values derived from the reports of Robelin (1975) in which Charolais bulls were used. However, because the differences in fat content between slaughter groups of the late maturing breeds are likely to be small, accuracy of measurement is essential since an error of 0·002 in carcass specific gravity can lead to a 1 % change in predicted fat content (Berg & Butterfield, 1976). Furthermore there are no relationships for the late maturing breeds which enable prediction of carcass composition from specific gravity. Subsequent studies in this series at Zürich should provide such information.

The upward shift in the realimentation between live-weight gain and ME intake/W$^{0.75}$ of the $RR_{II}$ steers is similar to the shift found in the trial of Meyer, Weitkamp & Bonilla (1965) and Fox *et al.* (1972). It is suggested that a fall in the energy value ($EV_g$) of the live-weight gain could have caused this shift. Any tendency to increase the protein : fat ratio, or the water : protein ratio (Ørskov & McDonald, 1976) would have such an effect. There were indications in the lamb trial that slightly more protein than fat may have been deposited during realimentation (Table 6) and that the $EV_g$ of refed steers may have decreased. If it is correct to assume a similar level of feeding and partial efficiency between control and realimented steers, then the decrease in $EV_g$ of realimented steers may have been the principal factor responsible for their improved energy conversion ratio during realimentation.

*Overall efficiency.* It is well established that the duration of the fattening period of sheep and cattle on a discontinuous growth path will exceed that of animals on a continuous growth path. However, the two trials reported here show that the associated increase in maintenance requirement was offset by a considerable reduction in the production

Table 10. *Gut fill, hot carcass weight, killing-out percentage and carcass specific gravity of steers*

| | | Restriction phase | | | Realimentation phase | | |
|---|---|---|---|---|---|---|---|
| | $C_0$† | $C_I$ | $RR_I$ | S.E. of the difference | $C_{II}$ | $RR_{II}$ | S.E. of the difference |
| Gut fill (kg) | — | 27·5 | 35·5* | 2·96 | 39·0 | 41·0 | 3·44 |
| Hot carcass weight (kg) | 116·0 | 162·4 | 164·1 | 7·68 | 255·9 | 253·7 | 8·98 |
| Killing-out percentage | 48·7 | 53·1 | 52·6 | 0·99 | 55·6 | 55·9 | 0·74 |
| Carcass specific gravity | 1·073 | 1·079 | ‡ | — | 1·074 | 1·076 | — |

† Initial slaughter group of six steers.
‡ Results discarded.
* Significantly different from control group ($P < 0·05$).

Table 11. *Duration for experiment, live weight, empty-body weight and growth performance of animals*

| | Restriction phase | | | Realimentation phase | | |
|---|---|---|---|---|---|---|
| | $C_I$ | $RR_I$ | S.E. of the difference | $C_{II}$ | $RR_{II}$ | S.E. of the difference |
| Duration | | | | | | |
| Lambs | 65 | 144 | — | 55 | 56 | — |
| Steers | 84 | 154 | — | 182 | 147 | — |
| Initial live weight (kg) | | | | | | |
| Lambs† | 23·0 | 22·5 | 3·34 | 32·7 | 31·6 | 2·55 |
| Steers | 237 | 236 | 6·3 | 306 | 315 | 8·8 |
| Final live weight (g) | | | | | | |
| Lambs† | 32·7 | 31·6 | 2·55 | 42·5 | 45·0 | 3·03 |
| Steers | 306 | 314 | 7·3 | 460 | 453 | 12·9 |
| Daily live-weight gain‡ (g) | | | | | | |
| Lambs† | 148 | 69*** | 0·9 | 189 | 219 | 27·2 |
| Steers | 884 | 539*** | 34·3 | 840 | 971* | 47·3 |
| Empty-body-weight gain (g) | | | | | | |
| Steers | 726 | 411*** | 25·4 | 783 | 871 | 46·4 |
| Energy conversion ratio (MJ ME/kg LWG) | | | | | | |
| Lambs | 72·2 | 88·1 | 12·18 | 77·7 | 68·0 | 8·94 |
| Steers | 56·0 | 79·9*** | 3·66 | 79·3 | 63·1** | 3·62 |

† Represent shrunk body weight.
‡ Calculated from linear regression of live weight on time.
* Significantly different from control group ($P < 0·05$).
** Significantly different from control group ($P < 0·01$).
*** Significantly different from control group ($P < 0·001$).

Table 12. *Total duration, daily body-weight gains, total energy intake and energy conversion ratio of lambs and cattle on a continuous and discontinuous growth path*

| | Lambs | | | Steers | | |
|---|---|---|---|---|---|---|
| | C | RR | S.E. of the difference | C | RR | S.E. of the difference |
| Days | 120 | 200 | — | 266 | 301 | — |
| Daily body-weight gains† (g) | 160 | 110* | 13·5 | 848 | 758* | 36·6 |
| Gross energy intake (GJ) | 2·23 | 2·49 | 0·107 | 28·04 | 28·04 | 0·488 |
| Metabolizable energy intake (GJ) | 1·46 | 1·67* | 0·077 | 16·14 | 15·43* | 0·274 |
| Energy conversion ratio (MJ ME/kg LWG) | 77·6 | 77·6 | 8·22 | 71·9 | 67·8 | 2·52 |

† Based on shrunk body weight and live weight in lamb and steer trial respectively.
* Significantly different from control group ($P < 0·05$).

requirement. Thus total gross energy intake and overall energy conversion ratio of the two groups of lambs and steers was similar (Table 12). This was possible because a moderate rate of growth of the control steers was chosen to maximize the intake of home-grown feeds (Thomson, Lehmann & Bickel, 1978).

It is concluded that at this level of intensity animals fattened on a discontinuous growth path, which involves a 'store' period followed by compensatory growth will not necessarily require a greater input of feed energy than animals on a continuous growth path. Including such a 'store' period enabled a reduction of the total concentrate input from 295 to 140 kg per steer.

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