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Compensatory growth in cattle - revisited

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ABSTRACT

Compensatory growth in cattle has been regularly reviewed (Allden, 1970; O'Donovan, 1984; Ryan, 1990) and factors influencing the recovery of liveweight sacrificed by a period of under-nutrition have been identified (severity and duration of under-nutrition, duration of the recovery period and age at restriction) but not quantified.

A data base representing 207 examples of compensatory growth in the literature was used to identify factors explaining the variance in recovered liveweight, unrecovered liveweight and % recovery in a general least squares linear model. Sixty percent of the variance in unrecovered gain was associated with the severity of the restriction but the recovered liveweight gain and % recovery was associated with only variables of the recovery period (liveweight gain of unrestricted group, 28%; liveweight gain of restricted group, 38% and duration of recovery, 14%). This focuses attention on the greater importance of the recovery period than the restriction period. Average % recovery was only 37% with a mean liveweight gain of the recovering cattle of 0.95 kg/d over 150 day recovery period.

We argue on theoretical grounds and with evidence that high levels of liveweight gain during recovery will only be achieved when an intense restriction has been imposed on older cattle and the recovery period has been long and at a high rate of liveweight gain.

Keywords: cattle; growth; compensatory growth; maturity.

INTRODUCTION

Compensatory growth is common in New Zealand's beef cattle industry. The incorporation of a period of lower feed intake in winter followed by compensatory, or "catch-up" growth in spring is consistent with a seasonal pattern of pasture production (Nicol and Kitessa, 1994).

New Zealand studies have contributed significantly to the literature on compensatory growth in cattle. Joblin (1968) was one of the first to demonstrate that an increase in feed intake (both absolute and relative) was a feature of compensation. The work of Everitt (Everitt 1972, Reardon and Everitt 1972, Everitt and Jury 1977) with young calves illustrated the lack of compensatory growth, at least in the medium term (to 18 months), following restricted growth in the first 10 weeks of life and Hight's classic experiments with breeding cows (Hight, 1966, 1968ab) clearly showed the remarkable ability of beef cows to recover liveweight lost during the winter over the following spring and summer.

There have been a number of scholarly reviews on compensatory growth (Allden 1970; O'Donovan, 1984; Ryan, 1990; Berge 1991) and these have identified, qualitatively, many of the factors influencing the very variable proportion of the liveweight deficit of the restrictively fed cattle that is regained during compensation. These factors include age at restriction, severity and duration of the restriction, rate of gain during recovery, length of the recovery period and quality of feed during recovery.

However, no attempt has been made to quantify the relative importance of such factors or to establish a general model which might help to explain the wide variability in the results of compensatory growth experiments. This paper reports on an analysis of the results of a number of compensatory growth experiments and formulates a working hypothesis of compensatory growth.

METHODS

From 57 literature citings on compensatory growth in cattle, the following details of 207 comparisons of two groups (restricted and unrestricted) of cattle were recorded: age (weeks) at start of restriction, genotype (British beef, British beef x, European x British, Friesian), mean liveweight at start of restriction (kg), sex (steers, heifers, bulls, mixed gender group), average liveweight gain of unrestricted group during restriction (kg/d), average liveweight gain of restricted group during restriction (kg/d), length of restriction period (d), liveweight gain of unrestricted group during recovery (kg/d), liveweight gain of restricted group during recovery (kg/d) and length of the recovery period (d).

Four further variables were calculated. These were: difference in liveweight (kg) between restricted and unrestricted groups at end of restriction (severity of restriction), unrecovered liveweight (kg) at end of recovery period, recovered liveweight (kg) at end of recovery period and % recovery (recovered liveweight as % liveweight difference at end of restriction).

The approach to identifying the relative importance of these variables to compensatory growth was to use either unrecovered liveweight, recovered liveweight or % recovery as the dependent variable in a general least squares linear model using breed and sex as fixed effects and liveweight gain of restricted and unrestricted groups over both the restriction and recovery period and the duration of both the restriction and recovery periods as variable effects fitted as covariates in the model. Non-significant ($p>0.01$) variables were progressively eliminated from the model.

In a further analysis, features of the restriction period plus the duration of the recovery period were considered as factors explaining variance in the difference in liveweight gain between the restricted and unrestricted groups during recovery.

RESULTS AND DISCUSSION

Table 1 gives details of the data and shows a large variation in all variables. Of note in terms of mean values is the relatively low value for the recovered liveweight (22 kg) and % recovery (37%). A simple correlation matrix of the variables showed few correlations above 0.5 between variables; the exceptions being; age and initial liveweight (0.71); liveweight gain of the restricted and unrestricted groups during restriction (0.68) and recovery (0.87).

TABLE 1: Mean and standard devlatlon of compensatory growth varlables (n – 207)

Variable	Mean	SD
Initial age (weeks)	36.7	40.1
Initial liveweight (kg)	209	87
Restriction period		
- liveweight gain (kg/d)		
unrestricted gain (kg/d)	0.716	0.382
restricted	0.226	0.350
- duration (d)	142	64
Recovery period		
- liveweight gain (kg/d)		
unrestricted	0.780	0.302
restricted	0.959	0.348
- duration (d)	148	82
Severity (kg)	64	38
Unrecovered liveweight (kg)	41	33
Recovered liveweight	23	23
% recovery	37	31

Table 2 highlights the proportion of the adjusted sums of squares accounted for by significant terms and identifies:

(i) severity of restriction as the dominant factor associated with variance in unrecovered liveweight with the three features of the recovery period (unrestricted gain, restricted gain and duration) also important.

(ii) no factors associated with the restriction period explaining significant variance in recovered gain or % recovery but liveweight gain of unrestricted and restricted groups during recovery and length of the recovery period are important sources of variance.

(iii) no significant effect of breed, age or initial liveweight.

Severity of restriction

Severity of restriction will have a large influence on unrecovered liveweight when the average % recovery is low as in these data (37%). For every additional 1 kg of restriction, 0.6 kg remained after recovery. Severity of restriction itself did not explain a significant proportion of the variance in recovered gain or % recovery but components of severity (liveweight gain of the unrestricted and restricted groups during restriction) did explain a considerable proportion of the variance (30%) in the difference in liveweight gain of restricted and unrestricted groups during recovery. The greater the difference in liveweight gain between groups during restriction, the greater the difference during recovery (+ 0.1 kg/d difference during restriction represents +0.06 kg/d during recovery). In other words, recovery was apparently greater from a short, sharp restriction than a long, slow restriction of the same severity.

TABLE 2: Proportlon of adjusted sums of squares accounted for by compensatory growth varlables In a general least square llnear model. (Values glven are for model excludlng non slgnlflcant terms).

Term	Dependent variable			
	Unrecovered liveweight	Recovered liveweight	% recovery	(Restricted-unrestricted) gain during recovery
Breed	NS	NS	NS	NS
Sex	1	0.2	2.0	NS
Age	NS	NS	NS	NS
Initial liveweight	NS	NS	NS	NS
Restriction period				
- unrestricted gain	NS	NS	NS	12
- restricted gain	NS	NS	NS	19
- duration	NS	NS	NS	NS
- severHy	60	NS	NS	NS
Recovery period				
- unrestricted gain	13	28	26	N/A
- restricted gain	16	38	25	N/A
- duration	5	14	5	10
Total variance accounted for by model	91	80	53	42

NS – not signiticant (P, 0.10) N/A – not applicable

Duration of recovery period

The model shows a decrease in unrecovered liveweight of 0.15 kg/each additional day of recovery although clearly this is not a strictly linear effect as the difference in liveweight gain between restricted and unrestricted groups during recovery decreases over the recovery period (Figure 1). The average recovery period was only 148 days with only 18% of trials extending recovery periods over 250 days suggesting that many compensatory growth trials have not exhausted the opportunity for compensation to take place.

Liveweight gain during recovery period

Clearly, the higher rate of the liveweight gain during the recovery period, the greater the total rate of liveweight gained over the recovery period and for every extra 0.1kg/d difference in liveweight gain between restricted and unrestricted groups during recovery, recovered gain increased by 10kg on average. However, is the difference in liveweight gain between the groups during recovery related to liveweight gain of the unrestricted group during recovery?

Our re-analysis of the data show some relationship, apart for very low liveweight gain of unrestricted groups during restriction, when the difference in liveweight gain is corrected for significant model effects (Table 1) (Figure 2).

FIGURE 1: Effect of duration of recovery period on difference in liveweight gain between previously restricted and unrestricted groups of cattle.

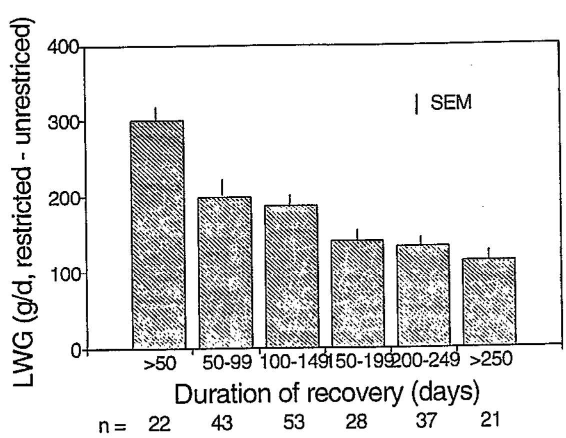
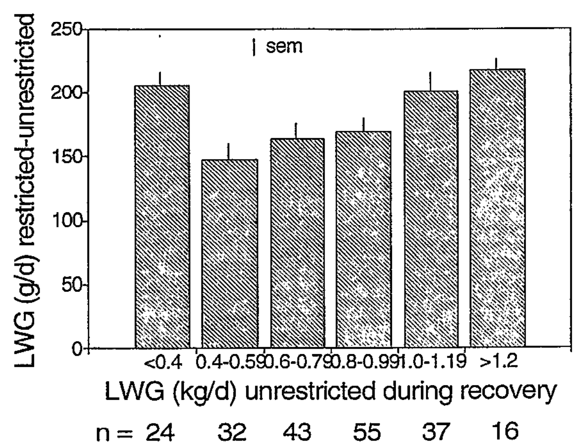


FIGURE 2: Effect of liveweight gain during the recovery period of previously unrestricted cattle on the difference in liveweight gain between restricted and unrestricted groups.



O'Donovan (1984) identifies liveweight gain during recovery as an important factor affecting the degree of compensation.

On the other hand, the difference in liveweight gain between the groups during recovery was related to the difference in liveweight gain between the groups during restriction (see above).

Age, initial weight and maturity at restriction

In this analysis age or initial liveweight was not a significant factor in explaining variance in compensatory growth. Proportion of maturity at restriction was calculated by dividing initial liveweight by mature liveweight (based on breed and sex). This variable failed to explain more variance than breed, sex and initial liveweight alone. Very few of the comparisons cited were made with animals over 1 year (10%) or under 3 months (4%) of age and this imbalance may well have prevented age or maturity from being identified as an important variable as it has in other reviews.

Although the analysis described here is somewhat of a "sledgehammer" approach, it does serve to focus attention on the recovery period rather than the restriction period as the critical feature of the "success" of compensatory growth. In general it would appear (Table 1) that research has been more effective at restricting growth (even the average liveweight gain of "unrestricted" groups during restriction was only 0.72 kg/d), than in providing conditions for high post-restriction liveweight gain (mean of 0.78 kg/d for unrestricted groups). Provision of appropriate conditions during the recovery phase is likely to achieve higher levels of compensation.

Towards a model for compensatory growth

In addition to providing an appropriate nutritional environment to promote compensatory growth during the recovery phase, the animals must be capable of exploiting the potential of compensatory growth. The potential of an animal to exhibit compensatory growth is likely to be a dependent on their stage of maturity and physiological and metabolic capacity for growth.

(a) the metabolic machinery

There is indisputable evidence that the mass of the digestive tract and organs such as the liver are reduced during restricted growth (O'Donovan, 1984). Associated with this decrease in mass and metabolic activity per unit mass, is a decline in total body metabolic rate and ME_m (/kg$W^{0.75}$) (see Ryan, 1990).

The regain in weight of such tissues, often with very high allometric growth coefficients (Young, 1988), will directly contribute to the early stages of liveweight recovery. Consequently, the protein:energy ratio in the regained tissues is higher than for unrestricted animals. Furthermore, it is claimed by some that this reduction in ME_m contributes to the increased feed conversion efficiency observed in compensating animals by increasing the ratio of ME_p:ME_m at any ME intake. A counter argument is that compensatory growth in carcass components (as opposed to realimentation of the GIT), is only likely to occur if the metabolic machinery has recovered to cope with a higher intake and higher rate of net protein synthesis and energy retention.

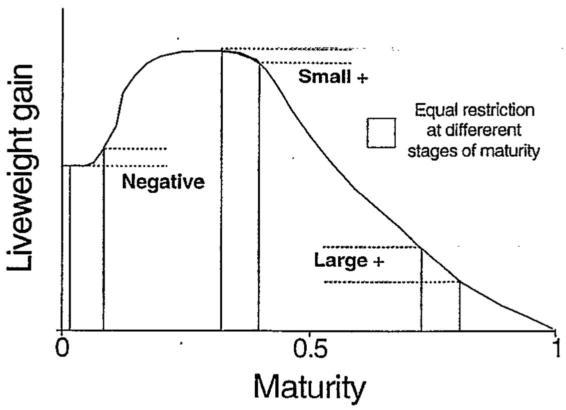
We argue that the higher levels of compensation identified with intense but shorter periods of under-nutrition as opposed to longer but less intense restriction (see above) may be because there has been proportionally less reduction in metabolic activity in the former case. Thus, although recovery of weight of tissues such as the liver and gut may be dramatic and contribute to initial rapid liveweight gain during compensation (see Figure 2), this phase of realimentation may be antagonistic to rapid regain of carcass tissues. More detail is needed on the relative contribution of the three pools of gut fill, organ mass and carcass mass to liveweight change during restriction and compensatory periods.

(b) stage of maturity

The general effect of stage of maturity on absolute liveweight gain is shown in Figure 3. If restriction in growth is considered to be a relative retardation in maturity, then the theoretical effect of a similar retardation in maturity is likely to depend on the stage of maturity where the restriction is imposed. A similar restriction in maturity will have a relatively large positive effect on potential liveweight gain in more mature cattle, a small and variable effect on animals at a stage of maturity close to their maximum liveweight gain and even a negative effect on liveweight gain in very young cattle. Part of the variability between the responses in compensatory growth trials could be due to the fact that most of the experiments have been made over a range of maturity where the response in increased liveweight gain is likely to be small and variable. More work is needed to clarify this point by directly comparing compensatory growth in cattle varying in stage of maturity at the start of the recovery period. Incidentally, the observation (see above) that cattle apparently recover better from a short, sharp restriction may be related to the fact that they will be more mature (over restriction and recovery) than groups subjected to a long slow restriction.

Numerous compensatory growth experiments with cattle have shown an increased feed intake (both per head and per $W^{0.75}$) during the recovery period although there is some debate as to whether intake is increased above that consistent with the reduced maturity of the restricted cattle. If the stimulus for increasing intake was proportional to the effect of the reduction in maturity on liveweight gain, then the feed intake of older cattle might be expected to be stimulated to a greater extent by a similar restriction in maturity than less mature cattle.

FIGURE 3: A schematic model of the effect of a restriction in maturity on potential liveweight gain.



CONCLUSIONS

This revisit of compensatory growth in cattle has, with a quantitative, if rather crude approach, identified that features of the recovery period after under-nutrition is of greater importance to the proportion of the liveweight deficit which will be recovered during compensation than features of the restriction period. Higher levels of liveweight recovery are likely to be achieved when the recovery period is long and supports high liveweight gain in older cattle recovering from a short, intense restriction.

We suggest there are good theoretical reasons related to stage of maturity and to the ratio and activity of GIT tissue to carcass tissue which support the above conclusion.

REFERENCES

Allden, W.G. (1970). The effects of nutritional deprivation on the subsequent productivity of sheep and cattle. *Nutrition Abstracts and Reviews* **40**: 1167-1184.

Berge, P. (1991) Long-term effects of feeding during calfhood on subsequent performance in beef cattle (a review). *Livestock Production Science* **28**: 170-201.

Everitt, G.C. (1972). Calf growth and lifetime performance of beef cattle. *Proceedings of the New Zealand Society of Animal Production* **32**: 20-25.

Everitt, G.C. and Jury, K.E. (1977). Growth of cattle in relation to nutrition in early life. *New Zealand Journal of Agricultural Research* **20**: 129-137.

Hight, G.K. (1966). The effects of undernutrition in late pregnancy on beef cattle production. New *Zealand Journal of Agricultural Research* **9**: 479-490.

Hight, G.K. (1968a). Plane of nutrition effects in late pregnancy and during lactation on beef cows and their calves to weaning. *New Zealand Journal of Agricultural Research* **11**: 71-84.

Hight, G.K. (1968b). A comparison of the effects of three nutritional levels in late pregnancy on beef cows and their calves. *New Zealand Journal of Agricultural Research* **11**: 477-483.

Joblin, A.D.H. 1968 Winter feeding trials with beef cattle. *Proceedings of the New Zealand Society of Animal Production* **28**: 145-156.

Nicol, A M and Kitessa, S M (1994). Influence of compensatory growth on production systems in New Zealand. Proc. Growth and Development Workshop, CRC Meat Quality, Armidale (in press).

O'Donovan, P.B. (1984). Compensatory gain in cattle and sheep. *Nutrition Abstracts and Reviews* **54**: 389-410.

Reardon, T.F. and Everitt, G.C. (1972). Effects of pre-weaning nutrition on subsequent growth rate, feed conversion efficiency and carcass composition of identical twin steers. *Proceedings of the New Zealand Society of Animal Production* **32**: 26-38.

Ryan, W.J. (1990). Compensatory growth in cattle and sheep. *Nutrition Abstracts and Reviews* **60**: 654-664.

Young, M J (1988). Bone and muscle growth in sheep. Unpublished PhD thesis, Lincoln University.