
VOLUME 62 2002

RELATIVE EFFECTS OF ENVIRONMENT AND LIVEWEIGHT UPON THE FEED REQUIREMENTS OF SHEEP

L. J. LAMBOURNE*

C.S.I.R.O. Division of Animal Physiology, Pastoral Research Laboratory, Armidale, New South Wales, Australia

SUMMARY

The feed intake corresponding to zero weight change has been estimated by suitable regression methods from records of the feed intake at pasture (by the chromium oxide/nitrogen technique) and in pens (by hand-feeding on cut pasture herbage). Adult New Zealand Romney Marsh and Australian fine-wool Merino wethers were studied over a wide range of liveweights resulting from differences in body condition of sheep of similar body size.

Maintenance requirements of the grazing sheep were in all cases higher than those of pen-fed sheep of the same weight. The increase was only 10 to 30% for heavy sheep grazing in good pasture, but amounted to 50 to 100% for the medium and low weight sheep maintaining weight in progressively poorer pastures.

The maintenance requirement of medium and low weight grazing Merinos was considerably reduced when their weight was controlled, not by continuous access to poor pastures, but by restricted access (1½ to 4 hours daily) to a good pasture.

The maintenance requirements of the pen-fed Romneys were similar to, and of the pen-fed Merinos were lower than, the amount specified by the usual ration scales and approximately equal to twice basal metabolism, while the requirements of the grazing sheep were generally a good deal higher, for both breeds.

The apparent increase in maintenance requirements, which was felt to be well outside possible experimental error or bias, roughly matched the increase in grazing time but seemed too great to be explained solely as energy spent in locomotion.

Energy expenditure might be higher in hard grazing conditions because of extra work performed in grazing from a very short sward, or through the existence of an adrenal, or similar, "stress" mechanism, causing increased heat production of metabolic or endocrine origin. Further work is planned to test these suggestions.

INTRODUCTION

THE INDIRECT METHOD of measuring pasture intake has been under test in several countries for many years, and a large body of evidence has been published by which to assess its value. It

*Formerly of Ruakura Animal Research Station, New Zealand.

is clear that the dilution of a constant daily or semi-daily intake of chromium oxide (Cr_2O_3) gives a fairly reliable estimate of the mean daily faeces output of an animal (Brisson, 1960; Raymond, 1954) and that the digestibility of the herbage eaten is closely enough related to the nitrogen concentration in the resulting faeces to make possible the estimation of feed digestibility, usually as the "intake factor", or ratio of feed/faeces, from a local regression equation derived from trials with similar herbage (Lancaster, 1954; Raymond *et al.*, 1954) though there are many potential sources of error or bias whose presence it may be exceedingly difficult to detect and eliminate (Raymond *et al.*, 1956; Corbett, 1960).

Although the resulting estimates of feed intake are undeniably less precise than might be wished, it is important to establish as soon as possible the main parameters of the utilization of grassland by grazing ruminants. Even approximate figures may help to focus attention on the aspect of applied physiology, of experimental technique, or of practical husbandry which may be seen to be of dominating importance. It should be an axiom of experimentation that a measurement technique, like a treatment effect, must be judged not only by absolute and therefore arbitrary standards but also against the general order of variability inherent in the system to be measured.

In an earlier attempt to examine the partitioning of the gross feed intake of grazing sheep (Lambourne, 1955) it was difficult to relate the observed weight changes and milk production of ewes to their estimated feed intake with any precision because there was no satisfactory way to calculate and deduct their apparently large maintenance requirement. In view of Wallace's (1956) evidence that the requirements of grazing cattle were appreciably higher than those of stall-fed cattle, it seemed unwise to rely on ration standards based originally on calorimetric experiments (Brody, 1945) or on pen-feeding trials (Wood, 1933), the experimental bases of which have recently been considered by Blaxter (1956, 1958, 1960), and Phillipson (1958).

An experiment was therefore conducted at Ruakura in 1956 specifically to determine the relationship between liveweight and maintenance requirement for pasture herbage of sheep kept in indoor feeding pens and of similar sheep grazing. The overall results of this experiment seemed unequivocal, but were so interesting in their implications that a confirmatory experiment was deemed necessary. This was carried out at Armidale in 1959 and 1960. Only the broader aspects of the two experiments are compared here.

EXPERIMENTAL

Animals and Management

Adult wethers were used—Romney Marsh in New Zealand and fine-wool Merinos in Australia.

In the first experiment, groups of six selected at random were grazed for several months so that they diverged to mean liveweights of nominally 80, 120, and 140 lb. Each group was then split—one sub-group of three was thereafter grazed and one fed in pens on cut pasture herbage so that their weights remained essentially constant for 11 months. The weight of the grazing sheep was regulated by movement to more or to less abundant ryegrass and clover pastures, or by adding or withdrawing extra non-experimental sheep, as required.

In the second experiment, random groups of seven, grazed over a period of 2 to 3 months to mean liveweights of nominally 60, 80, and 110 lb were split—one sub-group of five was grazed as before at constant weight, and a pair of sheep was kept indoors in metabolism pens and fed on cut pasture herbage at constant liveweight, for seven months. For a further 2 to 3 months the metabolism pens were placed outside, and the liveweight of the low weight and medium weight grazing sub-groups was regulated by allowing them 1½ to 2½ and 2 to 4 hours grazing per day respectively in the good pasture in which the high weight sub-group was grazing continuously.

It must be emphasized that the range in weight in both experiments consisted of differences in condition or of fatness of adult sheep of similar body size.

Measurement of Feed Intake

The intake of digestible organic matter (D.O.M.) by the pen-fed sheep was found from the usual samples of feeds, residues and faeces, taken and analysed by normal digestion trial methods.

The D.O.M. intake of the grazing sheep was estimated in consecutive 14-day periods by dosing with Cr_2O_3 and grab-sampling twice daily at about 8.30-9.00 a.m. and at 4.00-5.00 p.m. to estimate faeces output, and by using local regression equations found in 20 to 25 digestion trials to estimate the appropriate intake factor from the faeces nitrogen concentration.

From a large number of comparisons of actual with estimated D.O.M. intake, using the pen-fed sheep in these experiments, it was found that the standard error of estimate of D.O.M.

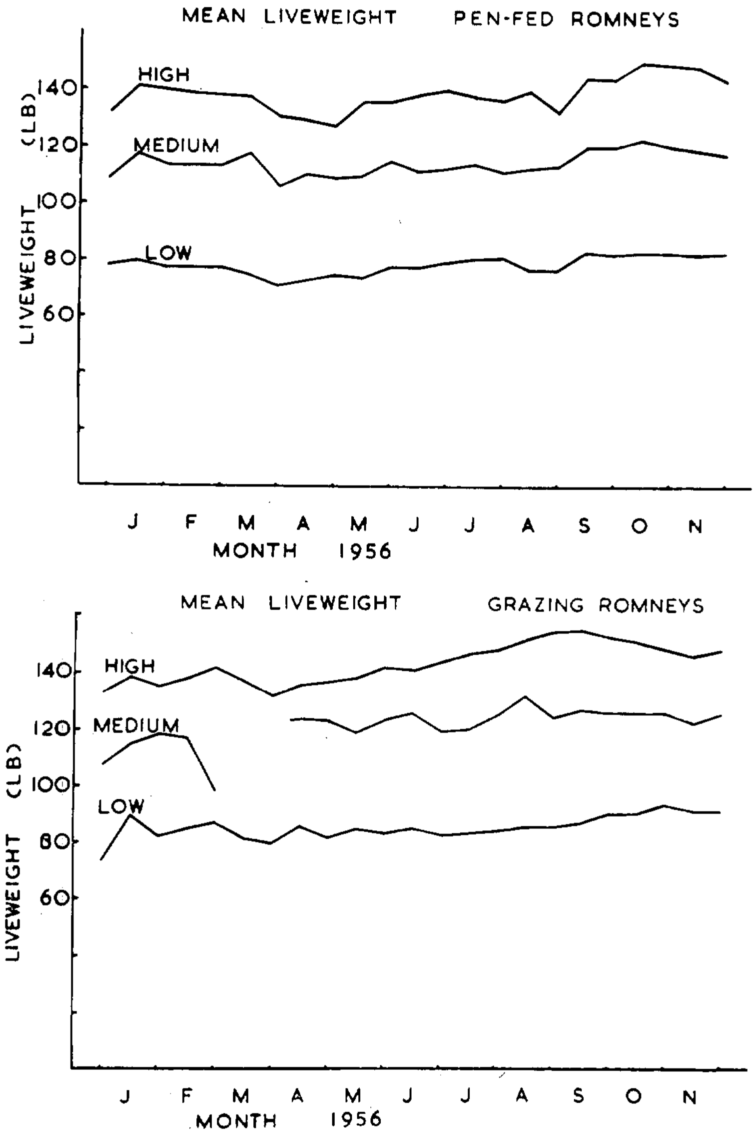

Fig. 1: Mean net liveweight of six sub-groups of Romney wethers over the eleven-month experiment, corrected for wool growth. All sheep in the original medium-weight grazing group died from facial eczema and were replaced.

intake was about 20% for a single sheep over 14 days. The error in estimates of mean D.O.M. intake of groups of 3 to 5 sheep should be about half this.

Measurement of Liveweight

All sheep were weighed two or three times weekly, depending on the weather. They were shorn at the start of the experiment and an attempt was made to keep essentially constant their net liveweight—observed weight minus estimated cumulative fleece weight. They were again shorn at the end of the experiment and their recorded weights corrected for their actual wool production.

RESULTS

New Zealand Experiment with Romney Wethers

Liveweight

The general constancy of group mean net liveweight is shown in Fig. 1.

Feed Intake and Maintenance Requirements

Estimates of feed intake may be studied in any of several ways—if liveweight remained truly constant the mean intake over a period might be taken as the maintenance requirement for the weight maintained. Where major fluctuations occurred, or an overall change of any magnitude, more precise information would be gained by calculating a relationship between weight change and mean intake in each period. The intercept made by this line at zero weight change would provide an estimate of the maintenance requirement for the mean initial liveweight. Figure 2 shows the mean weight change and feed intake of the sub-groups of three sheep in each 14-day measurement period.

The obvious feature of these results is that, despite the considerable errors implied by the scatter of the points, the general mean D.O.M. intake of the grazing sheep was considerably higher than that of the pen-fed sheep—by about 30% to 50% in the medium and high weight groups, and by about 80 to 100% in the low. While the mean intake of the indoor groups decreased steadily with liveweight, that of the grazing groups did not.

As Fig. 1 shows, the high weight grazing sheep made substantial gains in net liveweight over the later months of the experiment, and the least squares regressions of weight change on feed intake were calculated from the individual sheep data. These are shown as the broken lines in Fig. 2.

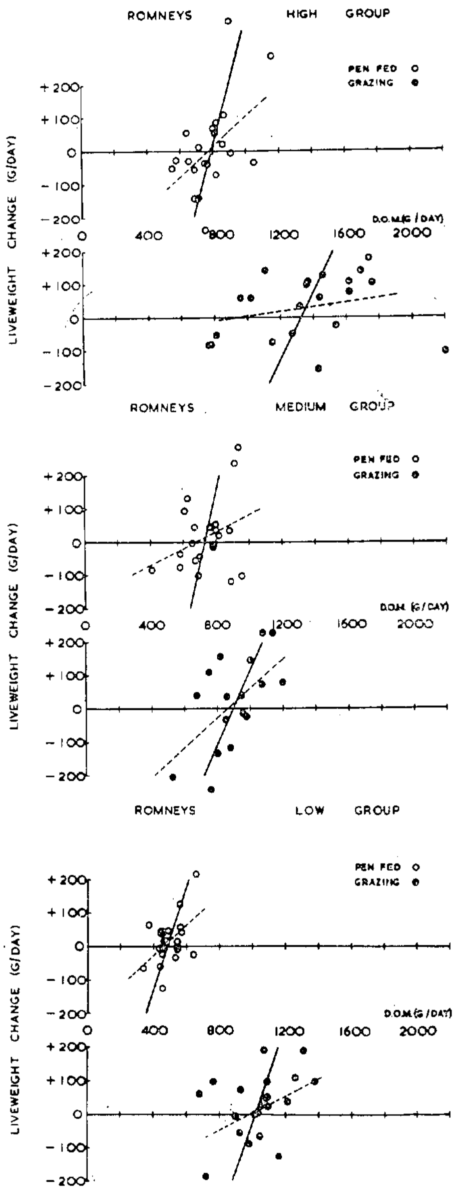

Fig. 2: Mean net liveweight change of Romney wethers shown as a function of mean D.O.M. intake, measured in 21 consecutive 14-day periods. Least-squares regressions, calculated from the individual observations, of weight change on D.O.M. intake shown with broken line and of D.O.M. intake on weight change shown with solid line.

Their intercept at zero weight change gives an alternative estimate of the maintenance intake, identical with the simple mean where no overall weight change occurred, but less or greater than the mean if there was an overall rise or fall in weight over the course of the experiment. The values obtained from these intercepts indicated that the maintenance requirement of the high, medium, and low weight grazing sheep had been higher than that of the indoor sub-groups by about 20, 30, and 100% respectively.

Further consideration made it clear that the use of this regression line in this way to estimate maintenance intake really implied that the rate of weight change was now being viewed as the independent variate, and that for this purpose the more correct procedure might be to use the corresponding regression of D.O.M. intake on weight change—these are shown as solid lines in Fig. 2.

The intercepts of these lines, however, yielded figures intermediate between the two previous sets, and did not alter the general interpretation at all.

None of these approaches was theoretically ideal though the latter two seemed more rigorous than the first—in reality the least squares method was inappropriate, for both variates were undoubtedly subject to very great, presumably random, error. Bartlett's (1949) method for two variates subject to error was next applied; this does not depend on variance calculations, but establishes a line through the general mean, as does the least squares method, but now with a slope determined by the general trend of the variates from the means of the two terminal thirds of the observations. This "functional relationship" gave a rather close approximation to the regression of Y on X or of X on Y, according as the observations were grouped on the X or the Y variate, and did not alter the earlier interpretation.

Kermack and Haldane (1950) discussed a method, earlier proposed by Karl Pearson, yielding the "reduced major axis" of the elliptical surface upon which the observations of two normally distributed correlated variables will lie—the line from which the sum of the squares of the deviations, measured at right-angles, is least. This reduces the data, with no specification as to the "independent variable", to a single line through the general mean of each variate, and of slope equal to the ratio of the separate standard deviations—that is to say, measured from the X axis the slope is (standard dev. Y)/(standard dev. X). The line in effect combines the regression of Y on X with that of X on Y, and necessarily lies between these two. It therefore gives intercepts intermediate between these two, but identical with them and with the general mean if overall weight change during the experiment is zero.

This seemed to be the method of choice, and was used throughout in obtaining final values of maintenance intake for further analysis.

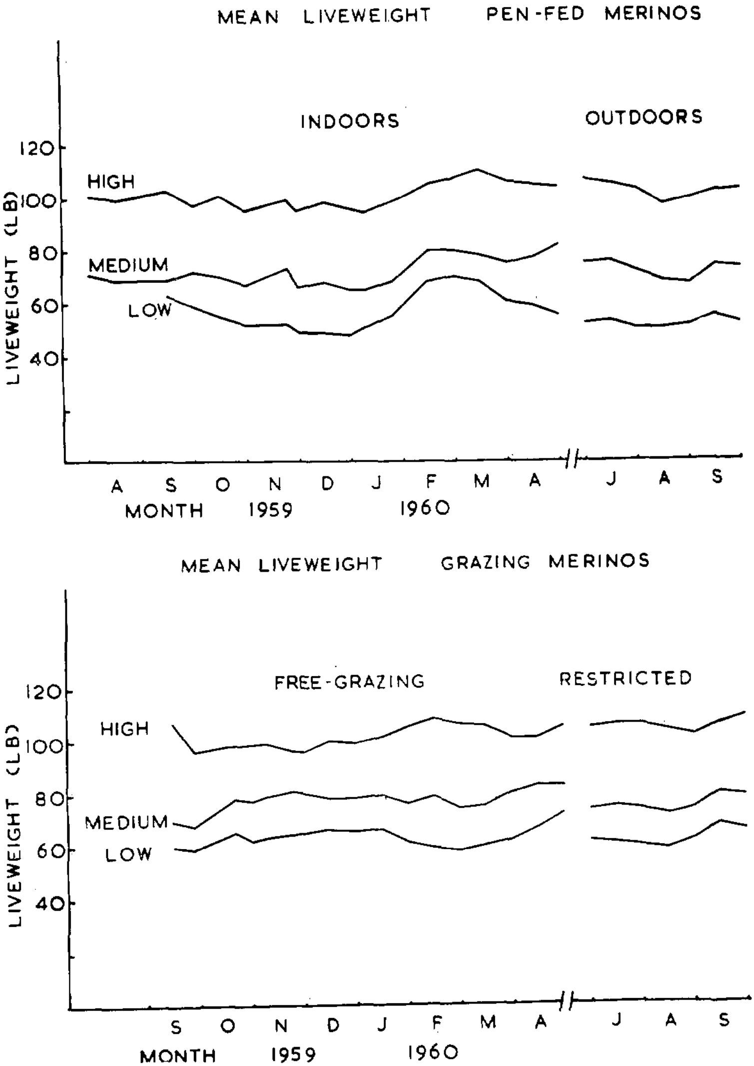

Fig. 3: Mean net liveweight of six sub-groups of Merino wethers in two main experimental periods, corrected for wool growth.

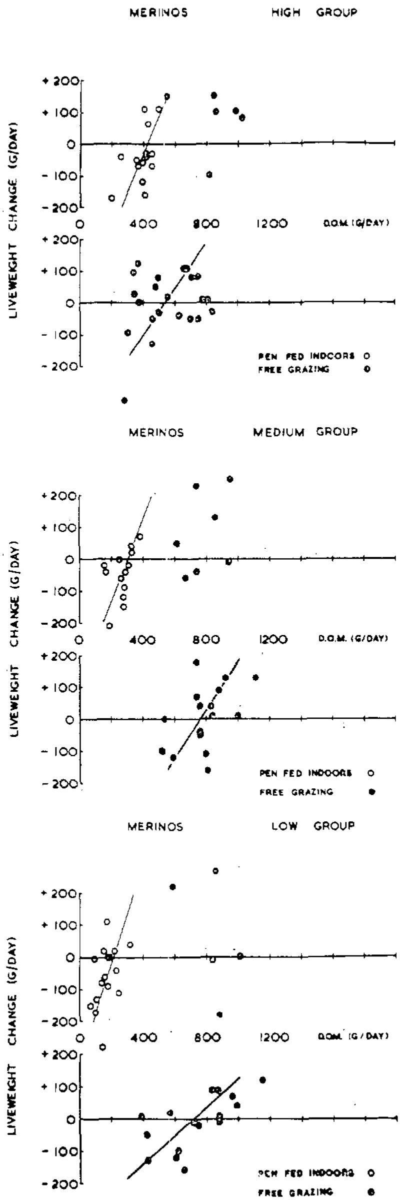

Fig. 4: Mean net liveweight change of Merino wethers shown as a function of mean D.O.M. intake, measured in consecutive 14-day periods, during the first stage of the experiment. The upper portion of each graph includes 13 or 14 points when these sheep were pen-fed indoors, and 6 or 7 when they were grazing outside with the corresponding free grazing groups. The line drawn is the reduced major axis of the correlation surface, calculated from the individual observations.

The apparent maintenance requirements of the grazing sheep—particularly the low weight group—were so much higher than those of the indoor sheep that corroboration was sought in the second experiment.

Australian Experiment with Merino Wethers

Liveweight Changes

An overall summary is given, again as group means, in Fig. 3. The pen-fed sheep were given a spell outside during part of January and February 1960 and some of their weight gains occurred in this period.

Feed Intake and Maintenance Requirements

First Stage: September 1959-April 1960

The results are shown, again as means for each group of (five) grazing and (two) pen-fed sheep, in each period, in Fig. 4.

The line drawn is the "reduced major axis" calculated from the pooled data for individual sheep, and its slope was used to correct the mean weight change and D.O.M. intake of each sheep, to give the most objective estimate of individual maintenance requirements.

Once again, and more clearly than before, the requirements of the grazing groups were found to be greater than those of the indoor-fed sheep of similar weight.

In four or five 14-day periods during the main experiment and in two at its conclusion, the weight changes and feed intake of the pen-fed sheep were determined while they were grazing outside with their counterparts. These points are shown in Fig. 4 and confirm that the higher apparent requirement at pasture was not an artefact due in the previous case to confounding of genetic and environmental differences.

The estimated *increases* in maintenance requirement at pasture above the indoor feeding levels ranged from 20 to 30% for the high weight sheep set-stocked in good pasture to about 200% for the low weight sheep which were subsisting on extremely close-grazed pasture. The former were found to be spending about 4 to 5 hours per day, and the latter 8 to 10 hours, grazing.

Second Stage: June-August, 1960

The liveweight of the grazing sheep in the medium and the low weight groups was regulated by allowing them restricted access to the good pasture in which the high weight group was set-stocked, and the three pairs of indoor sheep were transferred outside in their metabolism pens in mid-winter. During the two months there were frequent light snowfalls and almost continuous heavy frosts. The sheep had all been shorn in April. By trial and error it was found that the prescribed weights of 60 and 80 lb were maintained by about 1½ to 2½ and 2 to 4 hours grazing, but this was varied as required.

The results are shown in the usual way in Fig. 5, as group means for each measurement period for the medium and low weight sheep. The major axes found for indoor feeding and free grazing are redrawn to indicate those previous intercepts.

While the points are too few to establish very precise figures, it is clear that the transfer outdoors increased maintenance requirements a little (the high weight sheep, not shown, also confirm this) while the control of weight by restriction of grazing time on good pasture caused a substantial reduction in

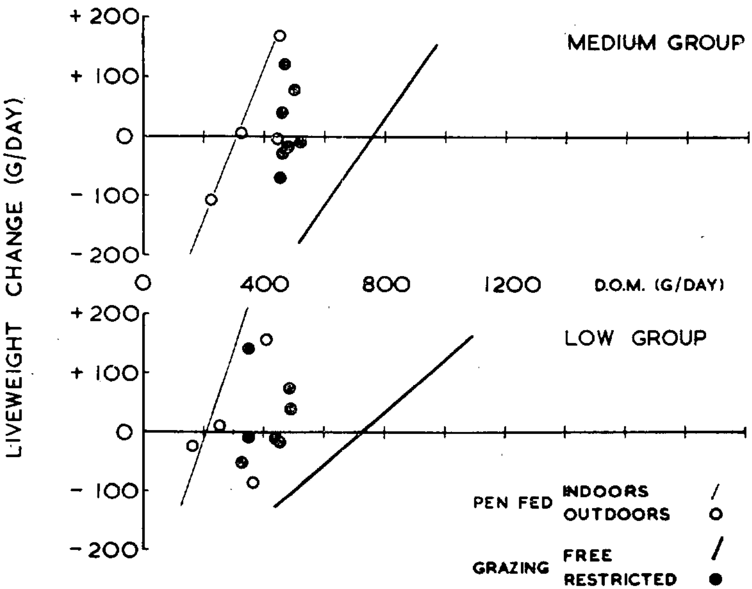

Fig. 5: Mean net liveweight change of Merino wethers shown as a function of mean D.O.M. intake, measured in consecutive 14-day periods, during the second stage of the experiment. Each open circle is for two sheep pen-fed outdoors, and the major axes established for the same pairs pen-fed indoors (Fig. 4) are shown for reference. Each solid circle is for five sheep allowed to graze for 1½ to 2½ hours per day (low weight), or for 2 to 4 hours per day (medium weight) in a good pasture, and the major axes established for the same sheep when free grazing in moderate and very short pastures respectively (Fig. 4) are shown for reference.

maintenance requirements below those found for free grazing on poorer pasture.

Both Experiments: Relationship Between Liveweight and Maintenance Requirement

New Zealand Romneys

The maintenance intake was determined for each animal and used to find the exponential relationship with liveweight by a least squares analysis of the logarithms, and the results are summarized in Fig. 6.

For the pen-fed sheep there was a significant linear regression with slope about 0.8. The three individual sheep within each grazing group were too few to give significant within group regressions but pooling of the data for the medium and high weight groups gave a significant regression with slope 1.6 and the (non-significant) relationship among the three sheep in the low group had a regression coefficient over 2.0.

Australian Merinos

Individual estimates were analysed after logarithmic transformation and the least squares regressions are also shown in Fig. 6 with the group means.

A significant linear regression over the full range of weights was given only by the indoor sheep, and its slope was 1.3. The individuals and the group means for outdoor pen-feeding and restricted grazing appeared to be linearly distributed, with slopes about 0.7 and 0.3 respectively, but the linear regressions were non-significant.

From the raw figures it is evident that maintenance requirement of the free grazing sheep had an overall *inverse* relationship to group mean liveweight, but within either the high or the medium group the relationship was positive though non-significant. The slopes were 0.9 and 1.0 respectively and are indicated in Fig. 6.

DISCUSSION

Validity of the Methods

It was stated earlier that an estimate of D.O.M. intake for an individual was likely to have an essentially random error of up to 20 to 25%, but there was no evidence in all the digestion trials carried out that this estimate would be seriously biassed. Particular care has been taken (Lambourne, unpublished results) to test whether the nitrogen regressions show any trend in error

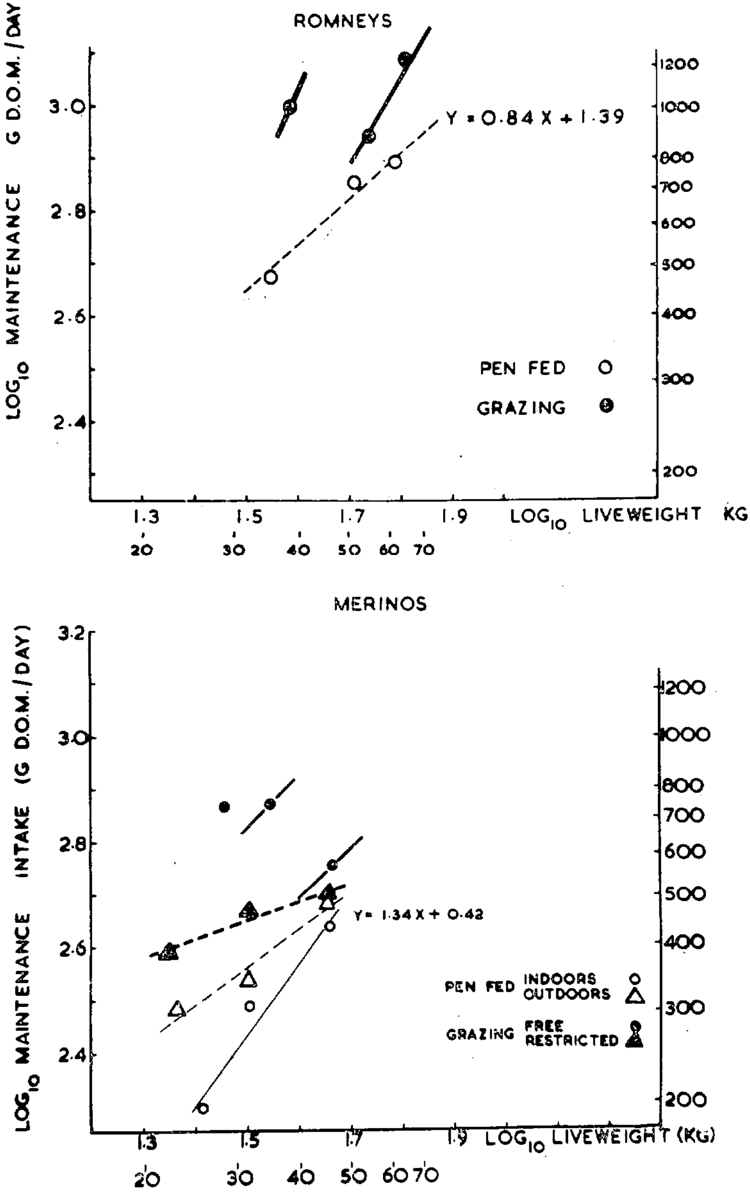

Fig. 6: Relationship between log maintenance requirement and log liveweight for Romneys and for Merinos. The untransformed values are indicated on auxiliary scales. The linear regressions were significant only for the indoor pen-fed sheep, and the equations are given for these. In other cases the (non-significant) linear relationships are shown over the range of weights in the group.

or in bias with increasing feed intake over the very wide range employed during these experiments. No such trend has appeared, but it is true that the highest levels of intake attained indoors have been lower than those found in the field.

If the error in the present measurements is random, sufficient measurements have been made to reduce it to negligible proportions. If there is not an error but a bias in estimates of D.O.M. intake of grazing sheep, it would need to be from +30 to +200%, to refute the general tenor of these results. No such bias has yet been demonstrated, or even suggested.

Influence of Liveweight and of Environment on the Maintenance Requirements of Sheep

The linear logarithmic relationships derived in the two parts of Fig. 6 are brought together in Fig. 7 to show maintenance requirement as a function of liveweight, in terms of the original units of measurement. For comparison, lines are drawn corres-

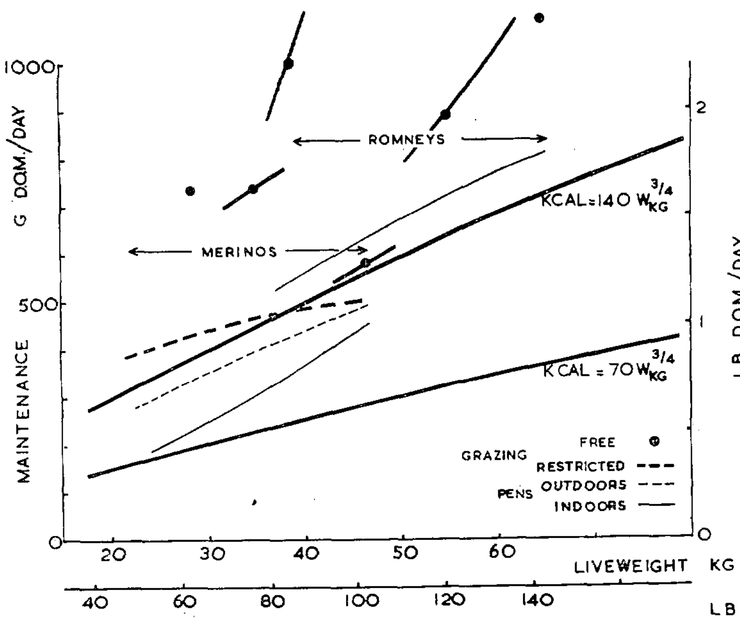

Fig. 7: Relationship between maintenance requirement and liveweight, for Romneys and for Merinos. Lines corresponding to basal metabolism and to twice basal metabolism, converted to equivalent intake on the arbitrary assumption that 1 lb D.O.M. equals 2,000 kilocalories of metabolizable energy, are shown for comparison.

ponding to Brody's (1945) equation for basal metabolism and to that for energy expenditure at maintenance taken as twice basal expenditure, both converted to equivalent intakes of D.O.M. on the assumption that 1 lb D.O.M. equals 2,000 kilocalories of metabolizable energy. This is an entirely arbitrary value for pasture herbage but follows Swift (1957) rather than Brody (1945) who used the figure 1 lb T.D.N. = 1,814 kilocalories.

The values obtained indoors for pen-fed Merinos were somewhat above the basal metabolism curve with the low weight group very close to it. These sheep were certainly very quiet and spent most of their time lying or standing motionless.

The values for Merinos pen-fed outdoors were below, and for Merinos on restricted grazing and for pen-fed Romneys, were all quite close to the "maintenance energy" calorimetric curve, and the general order of the exponent of liveweight was somewhat below 1.0.

There appears to be a difference, greater than experimental error, between the Romneys and the Merinos in the region 80 to 110 lb where their weights overlapped. This difference, ostensibly between the two breeds, may indicate only that a larger but thinner sheep needs more energy than a smaller fatter one.

All the values for free grazing animals were higher than the maintenance energy curve—the low weight groups particularly—and all had exponents above 0.8. Their distribution is so unsystematic, however, that it is not permissible to pool any of the groups for a more accurate determination of the exponent.

In general, these results suggest strongly that there may be no unique value for either the coefficient or the power of liveweight in the equation:

$$\text{Maintenance requirement} = k(\text{liveweight})^x$$

Rather there seems to be a whole family of curves, each describing the dependence of maintenance requirement on liveweight within a particular environment; each may be distinguished by a particular value of perhaps both k and x, and it appears possible that as the environment becomes more rigorous, the value of x may increase to above unity.

If this is so, it is to be supposed that curves for successively harsher environments must terminate at progressively lower liveweights, determined by the point at which the maintenance requirement, increasing as a power of liveweight perhaps greater than one, exceeds the physical capacity for food of a particular form of organs, musculature and metabolism.

Interpretation of Animal Production Experiments

Such a dependence of maintenance requirement on environment would go far towards reconciling the views of Wallace (1956), that the amount of feed used for maintenance by dairy cows in New Zealand was some 50% higher than the accepted stall-feeding standards, with those of Blaxter (1958) who felt that Wallace's estimate was too high, and of Holmes (1959) who concluded that the extra energy expenditure for grazing must be negligible; with the finding of Alder *et al.* (1960) that grazing beef cattle appeared to have requirements little greater than the stall-feeding allowance, and of Corbett (1960) that the maintenance requirement of his dairy cows were virtually the same when they were grazing as when stall-fed.

In attaining their very high rates of production per acre, dairy cows in New Zealand may encounter periods of quite severe nutritional hardship—either absolute or relative, as when they are "physiologically" under-fed in early lactation. Their annual average intakes, with which Wallace's equation dealt, could well include long periods when their maintenance requirements were, as the British workers find, only a little above those of stall-fed cattle. There would also be long periods when, extrapolating from the present results, their requirements might be higher by perhaps 60 to 80%, so that the overall average might well be increased by 50% as Wallace found.

Blaxter (1960) cites figures which indicate that the environment may considerably affect the energy expenditure of sheep, and seems to be persuaded that the existing calorimetric measurements are not an entirely adequate basis for determining the energy requirements of ruminants in more realistic situations (Blaxter, 1958).

Possible Reasons for Higher Maintenance Requirements at Pasture

It is difficult to see that the energy cost of locomotion can be great enough to explain these results. Similar increases in the apparent maintenance needs have been observed in other experiments (Lambourne, unpublished results) in circumstances which did not involve the performance of additional external work, but which suggest rather that there might be a substantial increase in heat production of primarily metabolic or endocrine origin, which might perhaps be described, loosely, as a "stress" reaction. There is no direct evidence that this was the case in the present experiments but it is an attractive suggestion which would be in keeping with the view of Reid and Hogan (1959) that pregnancy toxaemia in ewes may be associated with adrenal hyperactivity. It would be consistent, too, with the general practical experience that docile, contented stock "do" better, and with the effect of "gentling" on small laboratory animals, for example.

Further work is planned on this interesting question, which would neatly link some of the endocrine and metabolic functions of the ruminant, and would reveal the extent of their mutual dependence on characteristics of the grazing environment—a synthesis which has been too long neglected.

ACKNOWLEDGMENTS

The author wishes to thank Miss Helen McLean and J. P. E. Muller for their cheerful assistance with the experiment at Ruakura, and Miss A. E. Stevenson, under whose supervision the chemical analyses were carried out. The experiment at Armidale was carried out under the supervision of T. F. Reardon, and the chemical analyses were done by R. L. Rocks and D. J. Brett, to all of whom the writer is deeply indebted.

REFERENCES

ALDER, F. E., TAYLER, J. C., CHAMBERS, D. T., RICHARDS, J. A., RUDMAN, J. E. (1960): *Proc. 8th Internat. Grassl. Congr.*, p. 447.

BARTLETT, M. S. (1949): *Biometrics*, 5: 207.

BLAXTER, K. L. (1956): *Proc. Brit. Soc. anim. Prod.*, 3.

——— (1958): *Scientific Principles of Feeding Farm Livestock*, Proc. Conf., Brighton. Farmer & Stockbreeder Publications Ltd., London.

——— (1960): *Proc. 8th Internat. Grassl. Congr.*, p. 479.

BRISSON, G. J. (1960): *Proc. 8th Internat. Grassl. Congr.*, p. 435.

BRODY, S. (1945): *Bioenergetics and Growth.* Reinhold Publishing Corp., New York.

CORBETT, J. L. (1960): *Proc. 8th Internat. Grassl. Congr.*, p. 438.

HOLMES, W. (1959): *Measurement of Grassland Productivity*, p. 119. Proc. 6th Easter School in Agricultural Science, Nottingham University.

KERMACK, K. A., HALDANE, J. B. S. (1950): *Biometrika, 37*: 30.

LAMBOURNE, L. J. (1955): *Proc. N.Z. Soc. anim. Prod., 15*: 36.

LANCASTER, R. J. (1954): *N.Z. J. Sci. Tech., 36A*: 15.

PHILLIPSON, A. T. (1958): *Scientific Principles of Feeding Farm Livestock.* Proc. Conf., Brighton. Farmer & Stockbreeder Publications Ltd., London.

RAYMOND, W. F. (1954): *J. Brit. grassl. Soc., 9*: 61.

RAYMOND, W. F., KEMP, C. D., KEMP, A. W., HARRIS, C. E. (1954): *Ibid.*, 9: 69.

RAYMOND, W. F., MINSON, D. J., HARRIS, C. E. (1956): *Proc. 7th Internat. Grassl. Congr.*, p. 123.

REID, R. L., HOGAN, J. P. (1959): *Aust. J. agric. Res., 10*: 81.

SWIFT, R. W. (1957): *J. anim. Sci., 16*: 753.

WALLACE, L. R. (1956): *Proc. 7th Internat. Grassl. Congr.*, p. 134.

WOOD, T. B. (1933) [Revised by WOODMAN, H. E. (1952)]: *Rations for Livestock.* Bull. 48, Minist. Agric. H.M.S.O., London.