STUDIES ON THE NUTRITION OF GRAZING RUMINANTS

COLLECTED PAPERS

BY

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PREFACE

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The majority of the world's cattle and sheep obtain most of their feed by grazing, yet studies on housed ruminants and experiments on the growth of grassland herbage that exclude grazing animals outnumber direct investigations of animal production from pasture. Such studies are a legitimate approach towards, and make necessary contributions to, an understanding of the processes involved in pastoral systems, but in themselves they are not sufficient to gain a full appreciation of these processes which entail complex interactions between climate, soil, plant and animal.

Interactions between components of pastoral systems.

Research on the nutritional value of cut herbages and on the nutrient requirements of housed animals yields essential basic information but however detailed the results may be, they cannot be combined so as to allow the precise definition or prediction, establishment or amendment, of the nutrient intake or productive performance of a grazing animal. The animal's needs, the amount and quality of the feed that it chooses to eat, and even the use made of the energy and nutrients gained will vary with the type of feed available, the ease with which it is acquired, and with the ever-changing climatic conditions. The feed on a pasture that is available for consumption comprises the herbage that the animal has not eaten on previous occasions plus the gains by growth and minus the losses due to senescence and decay. The gains and losses and animal demand will very rarely, if ever, be in balance. Moreover, in what manner and to what extent the animal does eat at any particular time determines, often to a large extent, what it shall have to eat and so how it shall perform in the future. Grazing animals will exercise considerable freedom in their choice of diet even though restraints are imposed by management, and the day to day changes in the pasture alter the range of the choice open to them. In selecting their feed the animals may eat more of one species than of another, or more of one part of a plant than of another. This behaviour, due to individual characteristics of the animals and plants and other causes, will be reflected in the botanical and morphological composition of the subsequent growth of herbage. The rate and extent of the subsequent growth as a whole, within the limits imposed by the supplies of solar energy, water and plant nutrients, will reflect the extent to which grazing has reduced the photosynthetic area of the plants and, consequentially, the extent of their root systems. Grazing may also render the plants more vulnerable to extremes of climate, and the exposure of bare ground may promote the erosion of soil by wind or water. All changes in the plant canopy will be accompanied and will in turn be modified by changes in the microclimate of the sward, and in the soil moisture and temperature regimes. Alterations will also occur in the direction or rate of change in populations of organisms both above and below the soil surface, including bacteria, fungi, and invertebrata such as helminths. All these effects, and their consequences for plant and animal production, will be further compounded with those due to the trampling of plant and soil by the grazing animals, and to the irregular redistribution of plant nutrients in their excreta.

Nature of an effective programme of pastoral research.

The dynamic interactions inherent in pastoral systems will be only partially understood and characterized if investigations are confined to studies of isolated components of the systems, of the biology of ruminants and, separately, of plant growth. Two mutually dependent approaches are necessary: synthesis must accompany analysis.

Investigations of an analytical nature stem initially from reports and observations of an anecdotal and descriptive type. One or more variables in the system being examined are isolated for study by holding other variables constant so far as this is possible within the limits set by the current state of knowledge. As analysis proceeds and detailed knowledge accumulates the precision and complexity of the experiments can increase, but it becomes increasingly necessary to test in a wider context the validity of conclusions drawn from them. Attempts must be made to construct from the detailed knowledge a model that describes a significant part of the system as a whole and which, as with analysis, has to be developed through a regenerating cycle of hypothesis and test. The results obtained as each model is put to the test will reveal the existence of interactions between variables that were previously unrecognized or whose significance was not appreciated; it may be found that other effects were accorded undue emphasis. Further analytical studies are then to be made, but now these are based on informed observation and not simply on anecdote and description. The information that they yield should in turn allow the construction of improved models.

Quantity and quality of herbage in relation to animal production.

The first paper in this thesis (1)* is an assessment, made at the beginning of 1966, of the state of knowledge at that time of the nutritional value of grassland herbage. In considering indexes of nutritional value, information was drawn from a wide range of closely controlled, analytical, experiments but wherever possible the significance

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* Numbers in parentheses refer to the order in which the papers are presented as indicated on their top right-hand corners, and as shown in the list below.

of the indexes was assessed in a wider context and by appeal to the animal. For example, to what extent are the differences that are found between herbage species in digestibility, as between Lolium perenne and Dactylis glomerata, reflected in significant differences in the performances of animals that graze these species?

Information of this type even on much larger differences, such as those between pasture growth stages, was scanty in 1950 when I was appointed to the Rowett Research Institute to develop a programme of grassland research appropriate to the aims of the Institute, which were "the advancement of understanding of the energy and material requirements of animals of agricultural importance so as to enhance the quality and quantity of their production to meet the needs of man".* At this time it was generally assumed that data on the effects of various cutting regimes on the growth of ungrazed swards and on the nutritional value of the feed harvested were directly applicable to grazed swards. It was further assumed that management practices devised from such information would inevitably promote large increases in animal production. It was nevertheless recognized that production from British grasslands remained disappointingly low. When expressed as "utilized starch equivalent" the mean national output was estimated to be about 1900 kg/ha/year†, representing some 3500 kg of dry matter. In contrast, dry matter yields more than twice as great were commonly harvested by machine. It was

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* Cuthbertson, D. P. (1963). - In: "Progress in Nutrition and Allied Sciences". Edinburgh : Oliver & Boyd.

† Report of the Committee on Grassland Utilization (1958). London: Her Majesty's Stationery Office, Cmnd. 547.

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clearly necessary to account for the apparent wastage of over 50 per cent of herbage grown and to increase from this low level the utilization of British grasslands which provided, and continue to provide, 60 per cent or more of the total feed eaten by that country's cattle and sheep. Equally clearly, greater understanding of the processes affecting the efficiency of pasture utilization and of the resulting animal production could come only from a research programme that included detailed studies of animals at pasture.

The immediate difficulty was one that had for long hampered such work: how might the quantity and quality of the feed eaten by grazing animals be measured? In 1950, techniques for estimating the digestibility of grazed herbage from faecal composition, and for estimating faeces output from the dilution in faeces of inert reference substances administered to the animals, were of recent origin. Little was known about the precision and accuracy of the estimates of grazing intake that could be obtained by their use. I therefore defined as a prime objective of the research programme, the development and critical evaluation of such techniques.

Intake from a pasture had frequently been estimated by cutting sample areas before and after a period of grazing to determine the amount of herbage apparently removed by the animals. While the faecal index techniques were being examined, the cutting method was used in experiments on two problems that appeared to be of immediate importance. These were (a) the possibility that low animal production from pasture might be due to a qualitative defect in the diet as well as to a failure to utilize fully the herbage grown; and (b) that the annual production from an area of pasture, in any case, was determined largely by the production obtained during the normal grazing season, which often extended over no more than 6-8 months.

The herbage grown on intensively managed pastures usually provided lactating dairy cows, and other classes of livestock, with more than sufficient protein for their needs. It appeared likely that milk production by potentially high-yielding animals was limited primarily by the supply of dietary energy. Feeds of low protein content were therefore given to dairy cows grazing pastures where intake was not restricted by a low availability of herbage. It was found (2,3) that only small increases in milk yield were obtained because the consumption of these feeds was accompanied by a significant reduction in the amount of herbage eaten. It was concluded that additional feed could usefully increase production when pastures were so heavily stocked that there was insufficient herbage to meet the needs of the animals, but large amounts were used in Britain when good grazing was readily available and they were simply replacing a less costly feed, namely grazed herbage. It appeared that their use generally represented a mistaken attempt to adjust the notional value of the diet of the grazing cows so as to match estimates of their requirements calculated, inappropriately, from tables of feeding standards.

The highest costs in milk and beef production were incurred in winter, when the animals were often housed and hand-fed. It was possible that economies would be effected, especially during the rearing phase, if the grazing season could be extended through some or all of this period by saving the late-summer growth on suitably prepared pastures. The relative values of a number of herbage species for maintaining young dairy and beef cattle were examined in trials that continued throughout several winters, when it was found (4) that the species which gave the highest yields of cut herbage gave the poorest results in terms of animal performances. There were found to be several reasons for this apparently anomalous result. There was variation between species in the extent of wastage in the standing herbage during the winter, and in the acceptability to the animals of what remained as shown by variation in their daily intakes and in the percentage of the available herbage that was consumed. These differences in the selectivity and intensity of grazing were reflected in the amount of damage done by trampling; moreover the types of herbage that were most susceptible to such damage were also less easily grazed when under snow.

It was recognized that if the pasture management on a farm was modified to permit late autumn and winter grazing, there would be repercussions that involved the long-term management and use of all grasslands on that farm. Appropriate methods for the integration of winter grazing in farming systems were therefore developed (5,7). They were based on information gained from experiments on the production of herbage to be saved for winter use (5) and on the performance of cattle grazing such herbage (6). This information also indicated means by which the grazing season could be usefully extended for fattening cattle and milking cows.

Both series of experiments, the feeding of grazing dairy cows and the extension of the grazing season, clearly demonstrated that the amount of animal product to be obtained from a pasture could not be determined reliably unless it was grazed, and that estimates of productivity based simply on measurements of the amount of feed harvested by machine could be seriously misleading.

The reasons for the differences between the treatments in animal performance would not have been made clear without the estimates of intake made by the cutting technique, but an examination of the technique showed (8) that it was not sufficiently precise and accurate for use in closely detailed studies of the intake and utilization of herbage by ruminants. Moreover, it could not usually be made to give estimates of the intake of individual animals, but only of groups, and the intake of energy and nutrients could not be determined except by an unreliable process of calculation (1) based on the estimated chemical composition of the herbage thought to have been eaten. All these difficulties emphasized the need for dependable indicator techniques.

Development of techniques for estimating grazing intake.

Errors in indirect methods for estimating digestibility from faecal composition were identified and evaluated in a series of experiments where the excretion of nitrogen, plant pigments (chromogen), and later of material soluble in 0.2N HCl was studied (9,10,11,12). Continuous digestibility trial procedures were devised to assist this work (10,11), and nitrogen was shown to be the most generally satisfactory faecal index of digestibility (9,12).

To develop satisfactory methods for the estimation of faeces output, the passage of inert substances through the alimentary tract was studied. It was shown (13) that the water-insoluble substance chromium sesquioxide (Cr_2O_3) was excreted more evenly than the soluble polyethylene glycol because (14) the latter, in solution, moved more rapidly from the reticulo-rumen than feed residues. It appeared that Cr_2O_3 was the best chemical marker-substance available and reasons were sought for the variation in its concentration in faeces. It was found (15) that Cr_2O_3, when administered in a concentrated form in a capsule, failed to mix adequately with the contents of the reticulo-rumen and passed from this organ in advance of the feed residues that it was intended to mark. A method of administration was required that would result in the Cr_2O_3 being carried well into the rumen, and there released slowly into the ingesta. To this end, Cr_2O_3 was incorporated in a specially made paper and it was found (15,16) that compared with other methods of administration, variation in the excretion of Cr_2O_3 was significantly reduced when it was given as the paper. This finding was confirmed with grazing animals (17,18) in experiments where the errors associated with various regimes for sampling faeces were defined.

These studies of the faecal nitrogen and Cr_2O_3 techniques showed that if they were applied without a considerable knowledge of their limitations, they were likely to yield spurious results. Many of the errors associated with the sampling and analysis of faeces, and with the subsequent calculations of digestibility and faecal output, were found to be biasing and not simply random. It was shown that if precautions were taken to minimize these errors it was probable that the digestibility of the herbage grazed by a single animal over a period of a week could be estimated with a standard error of about ±1%, and that an estimate of the mean daily intake of digestible organic matter would have a standard error as low as ±6% (8,19). These values, which were later supported by the results of an experiment with grazing dairy cows (23), indicated the numbers of animals that would be required for the detection, at the 5% level of significance, of differences in the digestibility and intake of herbage due to differences between pastures (10).

Intake and utilization of energy by grazing animals.

When the indicator methods for estimating grazing intake had been developed to the point where they could be used with reasonable confidence, special attention was paid to the intake and utilization of energy by grazing cattle and sheep for it was clear (1,2,3) that generally their productivity was determined by the amount of energy available to them rather than by the amount of protein or other nutrients in the diet.

It could be expected that the net efficiency with which an animal converted the metabolizable energy of a feed to, say, milk or meat would vary little whether that animal was given the feed in a stall or obtained it by grazing. The gross efficiency of conversion was likely to differ between the two circumstances because of variation in the amount of energy expended in maintenance activities. The magnitude of the increase in energy expenditure due to grazing was examined by statistical analysis of data on feed intake, and animal liveweight and production. It was shown (19) that imperfections in the techniques for measuring intake could cause very large errors in the values obtained for the expenditure. The improved techniques that had been developed were used for studies on dairy cows and sheep close-folded on pastures that promoted positive energy balances in the animals, and in this respect were typical of British low-land pastures. The method of statistical analysis was refined. For both species of animal it was found (20,22) that the expenditure of energy in maintenance under these grazing conditions was some 20 per cent greater than the expenditure that would be incurred in stall-feeding. In order to make such a comparison with sheep it was necessary to define the maintenance requirements of this species when kept indoors. This was done both by a calorimetric procedure and by determination of the amounts of feed required to hold liveweights constant (21). The two sets of estimates were in good agreement and showed that the British standard values then generally accepted were in error.

In the course of the experiments with the dairy cows it was found (23) that their herbage intake varied directly with the digestibility of the feed, as had been demonstrated with stall-fed animals. It was also found that intake at a given digestibility was lower at the end of the grazing season than at the beginning. This result shed some light on the common practical observation that "autumn" pastures did not appear to sustain animal production as well as earlier growths of herbage.

In a further examination of this phenomenon, calorimetric studies were made of the net energy values of an early and a late season growth of herbage (24). The difference that was found between the herbages appeared to be consistent with the differences between them in water-soluble carbohydrate content, the digestibility of cellulose, the molar proportions of volatile fatty acids produced in the rumen, and the proportion of the gross energy lost as methane.

In 1963 I joined the Pastoral Research Laboratory of the C.S.I.R.O., Division of Animal Physiology, at Armidale, N.S.W. The purpose of this Laboratory, in a country where some 160 million sheep and 19 million cattle graze the whole year round, is to increase understanding of the processes in soil, plant and animal that together determine the productivity of the land and of the animals it sustains. The objects of the programme of research that I initiated were to determine, in a variety of controlled long-term pastoral systems supported by detailed studies on penned animals: (i) what grazing animals eat; (ii) in what forms the feed consumed becomes available to them for metabolism; (iii) for what purposes and in what amounts the energy and nutrients of the feed are used; and (iv) to study in both the short- and long-term the extent to which various pastures meet or modify the needs of the animals. This work, as with the work of the whole Laboratory, was linked primarily with problems concerning the sheep industry, and especially with wool production.

Productivity of breeding ewes.

Since each year in Australia many millions of ewes are engaged in breeding and rearing a lamb, it was surprising that very little was known about the effects of pregnancy and lactation on wool growth. Most of the information available had been obtained from the fleeceweights at shearing of ewes that had or had not reared a lamb. It was unsatisfactory because usually it did not distinguish the effects due to pregnancy from those due to lactation. In addition it had not been obtained in well defined nutritional conditions and so it did not show how the effects varied with feed intake. Studies were made on Merino ewes whose primary function was the production of wool and the breeding of replacement stock for wool-producing flocks. In an exploratory experiment (25) it was found that lactation caused a significant reduction in the amount of wool grown by ewes grazing good pastures although there was a large increase in feed intake. The effects of pregnancy as well as of lactation were then examined (26) with housed ewes given feed in constant amounts throughout the breeding cycle and it was found that the effects were not proportionately greater at one level of feeding rather than another. The reduction in wool growth was more marked than with the grazing ewes which could vary their feed intake as the physiological state changed but, as in the earlier experiment (25), it was noted that the average daily rate of wool growth increased rapidly when the lambs were weaned. This finding led to a study of the effects of variation in the length of lactation on the productivity of grazing ewes and, in consequence, on the immediate and long-term performances of their lambs which were weaned at various ages (26,27). To assist definition of the effects of treatments imposed on the ewes, and of their consequences in the nutrition of their lambs, a reliable technique for measuring the yield and composition of milk produced by grazing ewes was developed (28).

Stocking rate and production.

The effects of variation in the length of lactation on ewe and lamb were studied with ewes grazed continuously at three different stocking rates.

The effects of stocking rate on the production from a pasture are greater than any that will result from changes in the management of the grazing of a fixed number of animals. If a very low stocking rate is doubled, animal production per unit area may also be doubled if the feed supply is sufficient to maintain unimpaired the production per head, but in general each increase in stocking rate will be accompanied by a reduction in individual performance. The point at which this reduction is not at least compensated for by an increased production per unit area will almost certainly be higher if wool alone is to be produced than if the sheep are also to breed their replacements. With dairy cows, or in prime lamb and beef production, the optimum stocking rate may be well below the maximum attainable. It is possible that practices uneconomic at a low stocking rate, such as the provision of concentrate feeds for grazing dairy cows (2,3), may be worthwhile or necessary at the higher rates, but even if a high rate has a satisfactory outcome over a short period of time, it may be too high over a period of several years if it causes retrogressive changes in plant and soil which jeopardize continuing productivity. Effects of stocking rate have also to be studied over a long term so as to examine the effects of variation between years in climate. Difficulties associated with a high rate in drought might be acceptable if drought occurred on average, say, one year in ten.

The experiment on varying the length of lactation of grazing ewes provided a striking example of interaction between treatment and stocking rate (26,27). At the highest stocking rate of the ewes it was found that lambs might have to be weaned at an early age if they were even to survive, let alone grow satisfactorily. Quite different results were obtained at each of the other two stocking rates. In addition the patterns of lamb growth showed distinctive differences between years (27). Studies on the growth and on the development of rumen function in the young lamb were accompanied by studies on the onset of helminth infestation. It was found (29) that the onset was significantly delayed if lambs were weaned at an early age on to pastures reserved for them, that is before they had the opportunity to ingest large numbers of infective larvae due to the consumption of large amounts of herbage contaminated by the ewes.

Calorimetry, and metabolism in the rumen.

At high stocking rates the availability of herbage may be reduced to the extent that the grazing animals have great physical difficulty in obtaining their feed. When the energy cost of grazing good pastures was estimated (20,22) it was realized that higher values might be obtained when feed was scarce. There were a number of reports to this effect, some indicating as much as a threefold increase in the amount of feed required by an animal to maintain a given liveweight in difficult grazing conditions, compared with the requirement on good grazing or in stall-feeding. Because of the considerable number of uncertainties attending the calculation of energy expenditure from data on feed intake and animal liveweight and production (1), it was desirable that additional estimates should be made by some other means. If a more direct method of estimation were available it would be possible to study more closely the causes of variation in the energy expenditure of grazing animals. Techniques were therefore developed for measuring the oxygen consumption and carbon dioxide production of grazing sheep and a satisfactory and thoroughly tested system is now available (30).

The determination of the quantity and quality of feed consumed by grazing animals (8,9,10,11,12,19), of the losses of energy and nutrients in their faeces (13,14,15,16,17,18) and of their heat production and losses of energy in gaseous products of digestion (30), yields valuable information on efficiency of production. Knowledge must also be gained of processes intermediate between the consumption of feed and its outcome if causes of variation in efficiency are to be understood. A major part of the energy of the feed eaten by ruminant animals becomes available to them as the volatile fatty acids (VFA) acetic, propionic and butyric, and their rates of production in grazing sheep were measured by a technique in which radio-isotopes of the acids were infused into the rumen (31). It was found that the rate of production of each acid was significantly related to its concentration in the rumen for sheep grazing a variety of pastures, as well as for those given concentrate and roughage feeds. Further examination of the results showed that the amount of energy (kcal/day) supplied to a sheep as the three VFA could be predicted from the 24h mean value for the total VFA concentration as determined by steam distillation of ruminal liquor (30,31).

Conclusion and integrating summary.

The technique used for the measurement of VFA production, which disclosed the significance of ruminal concentration and so opened up a new line of attack on problems of the nutritional value of herbage and of animal productivity, is only one of the wide range of research techniques now used on confined animals. Many more must be applied to grazing animals, with modification as necessary, so that the effects of treatments can be fully assessed. If assessments are made only in terms of the amount of milk, meat or wool finally obtained, a procedure that should be no more acceptable in the field than it now is indoors, it is unlikely that the information gain can be widely applied because it is unlikely that general principles will be established; nor may it be seen that work done on one problem bears on another because it is not recognized that the problems have common roots.

Great care must be taken in defining the objectives of a grazing experiment and in its design, because the establishment and execution are likely to be very costly. In addition to material requirements, such as good fencing and the provision of suitable yards supplied with electric power etc., there will be heavy demands on labour for routine management as well as for experimental requirements. For example, it is considerably more difficult and time-consuming to maintain fistulated animals in good condition at pasture than it is indoors and the determination of feed intake, which may readily be achieved with housed animals, is a major undertaking in the field. Moreover, the large outlay may be wasted if insufficient thought has been given to the types of measurement that should be made and the techniques required have not been prepared, and if actions that would be taken to meet various contingencies were not clearly defined at the time the experiment was designed. For example, if the animals on one area of pasture became seriously short of feed, should the numbers be reduced on this area only and not on the others in the experiment, or should supplementary feed be given to that group or to all groups when either action is likely to cause major alterations in the nature of the comparisons being studied? If such problems have not been anticipated the original experiment may become no more than a test of farming ability.

Grazing experiments must also be supported by facilities for experiments of an analytical type so that problems they bring to notice can be examined and resolved appropriately. Thus the suitability for winter use of one type of pasture (4) led to a detailed study of methods of managing that pasture (5) and subsequently to the development of a satisfactory system for out-wintering cattle (6,7); uncertainty about the reliability of indicator techniques for estimating grazing intake led to detailed studies of relationships between feed digestibility and faecal indexes (9) and of the passage of inert materials through the alimentary tract (13,14), and then to improved techniques (10,15,16) which were applied in several experiments (19,20,22,23) when opportunities for further studies were accepted (11,12,17,18,24); observations on the wool growth and feed intake by lactating ewes at pasture (25) were followed by the examination in well controlled conditions of effects of reproduction on wool growth (26), and led to investigations on the nutrition and growth of the young lamb (26,27,28,29); dissatisfaction with methods available for estimating the energy expenditure of grazing animals (20,22), stimulated the development of techniques of indirect calorimetry that can be used in the field to study this and many other problems (30,31).

The study in depth of a process followed by the application of the findings in a larger context should in turn promote further detailed research, and so on. This progressive cycle, once it is entered, will lead to a greater understanding, and will assist the management to greater advantage, of the complex events that follow the simple action of putting an animal on to a pasture to graze.

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I have been lucky to work in organizations where I could readily consult colleagues who were specialists in particular facets of my work. My thanks are due especially to Mr. I. McDonald of the Rowett Institute's Department of Biometry and to its Head, Mr. A. W. Boyne. Their expertise clarified many problems of experimental design and of the interpretation of results.

The tempo of the programme of research that I established at Aberdeen was much increased when Dr. J. F. D. Greenhalgh and Dr. J. P. Langlands joined my Section, for three-year periods from 1956 and 1959 respectively, to study for the degree of Ph.D.. Though I was officially their Supervisor, in practice their stays with me were most enjoyable and fruitful periods of collaboration, and the same is true of my present supervision of Mr. B. A. Young. I have received much help, in a variety of ways, from my colleagues in C.S.I.R.O. at Armidale, especially Mr. W. H. Southcott, and from Dr. R. A. Leng of the University of New England.

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Finally, I would like to acknowledge my debt to my tutors, first at the University of Reading and then in post-graduate work at the (then) Massey Agricultural College. In particular, study under the supervision of Professor I. L. Campbell and his colleagues at Massey first stimulated my interest in pastoral research.

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20. An estimate of the energy expended for maintenance by strip-grazed dairy cows. Corbett, J. L., Langlands, J. P. and Boyne, A. W. (1961). Proc. VIIIth int. Congr. Anim. Prod. Hamburg. III, pp.245-7.

21. Estimates of the energy required for maintenance by adult sheep. 1. Housed sheep. Langlands, J. P., Corbett, J. L., McDonald, I. and Pullar, J. D. (1963). Anim. Prod. 5, 1-9.

22. Estimates of the energy required for maintenance by adult sheep. 2. Grazing sheep. Langlands, J. P., Corbett, J. L., McDonald, I. and Reid, G. W. (1963). Anim. Prod. 5, 11-16.

23. Effects of season of growth and digestibility of herbage on intake by grazing dairy cows. Corbett, J. L., Langlands, J. P. and Reid, G.W. (1963). Anim. Prod. 5, 119-129.

24. Comparison by direct animal calorimetry of the net energy values of an early and a late season growth of herbage. Corbett, J. L., Langlands, J. P., McDonald, I. and Pullar, J. D. (1966). Anim. Prod. 8, 13-27.

25. Effect of lactation on wool growth of Merino sheep. Corbett, J. L. (1964). Proc. Aust. Soc. Anim. Prod. 5, 136-140.

26. Effects of pregnancy, length of lactation and stocking rate on the performance of Merino sheep. Corbett, J. L. (1966). Proc. Xth int. Grassld. Congr. Helsinki. pp.491-495.

27. Early weaning and its effects on Merino wool production, Corbett, J. L. (1967). Wool Technol. Sheep Breed. (in press).

28. Variation in the yield and composition of milk of grazing Merino ewes.
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29. Age of weaning and parasitism in Merino lambs.
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30. Measurement of energy expenditure by grazing sheep and of the amount of energy supplied by volatile fatty acids produced in the rumen.
Corbett, J. L., Leng, R. A. and Young, B. A. (1967).
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31. Rates of production of volatile fatty acids in the rumen of grazing sheep and their relation to ruminal concentration.
Leng, R. A., Corbett, J. L. and Brett, D. J. (1967).
Br. J. Nutr. (in press).

The following papers (32-43) are submitted in support of the principal publications presented in this thesis. They are entered in chronological order and comprise preliminary communications, reviews, and other papers relevant to the main theme.

32. Grazing behaviour in New Zealand. Corbett, J. L. (1953).
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33. Winter grazing of cattle in the north-east of Scotland.
Corbett, J. L. (1954). Proc. Br. Soc. Anim. Prod. pp.17-25.

34. Some aspects of the nutrition of grazing dairy cows.
Corbett, J. L. (1955). In: "Animal Production from Grass". *Eur. Ass. Anim. Prod*. Publ. no.6. pp.143-8.

35. The use of polyethylene glycol as an inert reference substance for the estimation of faecal output. Corbett, J. L., Miller, T. B., Clarke, E. W. and Florence, E. (1956). *Proc. Nutr. Soc*. **15**, v.

36. Seasonal variations in the nutritive value of grassland herbage.
Corbett, J. L. (1957). *N.A.A.S.q. Rev*. no.37, pp.1-9.

37. Evaluation of faecal nitrogen as an index of herbage digestibility by means of a continuous digestibility trial. Greenhalgh, J. F. D., McDonald, I. and Corbett, J. L. (1959). *Proc. Nutr. Soc*. **18**, xvii.

38. Further studies on the administration of chromium sesquioxide as a component of paper. Corbett, J. L., Reid, G. W., Langlands, J. P. and Florence, E. (1960). *Proc. Nutr. Soc*. **19**, xx.

39. The feeding of livestock. Corbett, J. L. (1961).
Jl. R. agric. Soc. **122**, 175-186.

40. The feeding of livestock. Corbett, J. L. (1962).
Jl. R. agric. Soc. **123**, 157-167.

41. Intake and utilization of herbage by grazing ruminants.
Corbett, J. L. (1963). In: "Progress in Nutrition and Allied Sciences" pp.171-7. Edinburgh : Oliver & Boyd.

42. Energy expenditure of grazing sheep estimated from oxygen consumption. Young, B. A. and Corbett, J. L. (1966). Proc. IXth int. Congr. Anim. Prod. Edinburgh. (in press).

43. Rate of production of volatile fatty acids in the rumen of penned and grazing sheep. Leng, R. A., Brett, D. J. and Corbett, J. L. (1966). Proc. VIIth int. Congr. Nutr. Hamburg. V, p.520.