HILL FARMING RESEARCH ORGANISATION

FOURTH REPORT

1964-1967

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HILL FARMING RESEARCH ORGANISATION

FOURTH REPORT

1964-67

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CURRENT RESEARCH PROGRAMMES

Agronomy Department

I. A. NICHOLSON *Head of Department*	Effects of intensive grazing on vegetation with special reference to plant succession. Hill Pasture Improvement study (Lephinmore). Hydrology and nutrient balance of peat catchments (in collaboration with Macaulay Institute).
J. S. BLACK	Soil and plant nitrogen in relation to seasonal growth of hill pastures under intensive grazing.
J. EADIE	Digestibility/intake relationships on bent-fescue pasture, with particular reference to intensive grazing.
M. J. S. FLOATE	Influence of intensive grazing on nutrient cycling in hill soils. The effect of past land use on soil development and current soil status.
J. N. PEART	Lactation studies. Intensive summer grazing.

Department of Animal Studies

J. M. DONEY *Head of Department*	Response to climatic exposure. Wind-tunnel studies. Nutrition and wool production.
W. N. M. FOSTER	Aetiology of tick pyaemia. Physiopathology of tick-borne fever.
J. G. GRIFFITHS	Response to climatic exposure. Wind-tunnel studies.
R. G. GUNN	Early growth and lifetime production. Effect of removal of nutritional limitations on ewe productivity.

A. J. F. RUSSEL	Metabolism of undernourishment.

Department of Botanical Studies

J. KING *Head of Department*	The relationship between growth rate and leaf area at various nutritional levels. Moorland management.
Miss S. A. GRANT	Investigations of the time of initiation and of cessation of growth of hill species in relation to temperature. Moorland management.
J. A. ROGERS	Relation between plant growth and soil moisture and nutrients in the hill environment.

RESEARCH STATIONS

THE three research farms continue to function under their respective Officers-in-Charge, Mr. A. L. Fairlie (Glensaugh), Mr. D. C. Currie (Lephinmore) and Dr. R. H. Armstrong (Sourhope).

Glensaugh is situated at the eastern end of the Grampians. It consists of some 2200 acres of rough hill grazings dominated by heather and ranging from 450 to 1600 feet, with 250 acres of short and long term leys and 75 acres of forage crops. Average rainfall is 41 inches. The breeding stock consists of 880 Blackface ewes and 110 hill cows.

Lephinmore is situated on the east side of Loch Fyne in Argyll. It consists of some 2800 acres of hill grazings up to 1550 feet altitude, mostly over peat, and with a mixed herbage including heather, *Molinia*, *Scirpus* and hill grasses. There are 75 acres of short and long term leys. Average rainfall is 67 inches at sea level. The breeding stock comprises 750 Blackface ewes and 35 hill cows.

Sourhope lies 15 miles south of Kelso on the western slopes of the Cheviot. There are 2650 acres of hill grazings at 600 to 2000 feet, consisting largely of grasses such as the *Agrostis* and *Festuca* spp., with substantial areas dominated by *Nardus* and *Molinia*. There are 125 acres of short and long term leys. Average rainfall is 30 inches. The breeding stock comprises 720 South-country Cheviot, 350 North-country Cheviot and 430 Blackface ewes and 25 hill cows.

INTRODUCTION

THIS fourth report of the Hill Farming Research Organisation is presented in a form rather different from that of previous reports. It is not simply an account of all research done in the last three years. Rather is it a summary of those parts of the Organisation's research work which, when taken as a whole, provide the background to the current research programme and indicate some of the directions in which future research will go.

Hill sheep farming, which is what the report is concerned with, has become a high cost—low output, and hence inefficient, system. It will survive only if production costs can be reduced or the efficiency of production increased. The former alone is likely to be sufficient only in the short term; the long term objective must be to increase the efficiency of production, either per animal or per acre.

Present limitations to production and its efficiency are largely inherent in the pastoral system itself, that is, in the management, or lack of it, of the natural resources of soils and vegetation. Additional economic inputs, for example, of feed and fertiliser into the present pastoral system are not likely to alone provide adequate answers. They, together with other frequently advocated measures such as off-wintering and fattening of lambs by hand-feeding, will make their greatest contribution within new pastoral systems characterised by higher soil fertility, better pastures and greater production per ewe.

The Organisation's resources are therefore now almost entirely devoted to research directed at new systems of pasture management and increased productivity per ewe. It must be emphasized that this does not mean simply the sowing of improved pastures on heavily fertilised hill ground and the replacement of the existing breeds by apparently more productive ones. Such measures do not represent a logical economic starting point, although they will no doubt find a place in due course.

The deficiencies in fertility of hill soils are largely a function of the parent rocks and the climatic conditions, but the influence of the grazing animal can be substantial, and investigations have recently begun (Section 1). The botanical make-up of hill vegetation is dependent on highly variable soil conditions, but the grazing preferences of the animal under free-grazing conditions play a major part (Section 2). Climate controls the seasonal pattern of pasture growth (Section 2) and this pattern, in the presence of low stocking rates and selective grazing, gives a year-round level of nutrition which is low (Section 4). Lifetime productivity per ewe is low (Section 6) and lamb growth rates are poor (Section 8). The nutrient requirements in late pregnancy are high and are not met by hill pastures; most of the ewe's body reserves are utilised during winter (Section 7).

Yet undernourishment in late pregnancy does not preclude high levels of milk production from ewes well fed during lactation (Section 8), while improved winter feeding has little effect on wool production (Section 9). Since improved production per ewe, either in terms of number of lambs produced or in growth rate of lambs, is dependent on better nutrition in autumn, spring and summer (Sections 6 and 8), winter nutrition becomes of less importance as nutrition in these periods is improved (Section 6).

Controlled grazing, particularly in spring, summer and autumn, can lead to substantial modification of the vegetational environment (Section 5) and this can have a major effect on the quality of the pasture and the nutrient intake of the grazing animal (Sections 3 and 4). The seasonal pattern of pasture growth will still be largely dependent on temperature and light and, within many hill farms, on altitude (Section 2). Increased grazing pressure and pasture utilisation can be expected to alter the soil-plant-animal nutrient cycle and hence soil fertility (Section 1).

Finally, the transition from present hill pastures to pastures of higher nutritional value via control of grazing can be hastened, or taken further, by the use of herbicides to remove unwanted vegetation, the introduction of new species of grasses etc. and these measures pose new botanical problems (Section 2).

Special areas of study include the physiological responses to climatic exposure, with particular reference to adaptation of hill breeds of sheep to their winter environment (Section 10) and the investigation of the tick-borne diseases, tick-borne fever and tick pyaemia (Section 11).

This brief summary shows how the various parts of a widely-based research programme fit together. At the centre of the research are the problems of the grazing animal in relation to the soil, vegetation and climate; this work is supported by basic and applied studies, usually under experimentally-controlled conditions, within the scientific disciplines of plant and animal nutrition and physiology.

There are many important gaps in the research programme and these are unlikely to be filled until our own laboratories and ancillary facilities become available in about two years' time. It is only through the generous assistance of the Edinburgh School of Agriculture, the Animal Breeding Research Organisation and the Scottish Plant


SITUATION
OF
RESEARCH STATIONS
SCOTLAND
ABERDEEN
GLENSAUGH
LEPHINMORE
EDINBURGH
GLASGOW
SOURHOPE
CARLISLE
NORTHERN
IRELAND
EIRE
ENGLAND
WALES
LONDON
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Breeding Station that facilities have been obtained in the last three years to enable much of the work of that period to be done.

Staff

In addition to the staff listed as at March, 1967, the following served for varying periods on the Scientific Staff during this triennial period:—

A. R. WANNOP, O.B.E., B.ENG., B.SC. (AGR.), F.R.S.E. Director.

Botanical Studies

A. D. MCKAY, B.SC. (AGR.)

R. F. HUNTER, B.SC. (AGR.), PH.D.

V. M. SHORROCKS, M.A., D.PHIL., M.I.BIOL.

Mr. A. R. Wannop, Director of the Organisation since its formation in 1954, retired on 30th September, 1965. He was Director of the Organisation during its difficult formative period. Under his guidance the first stages of the Organisation's research were completed. The basic information necessary for an assessment of the underlying scientific problems of hill farming was obtained and now forms the essential background to present research objectives. His sympathetic and kindly approach was a constant encouragement to the scientific staff.

Visits

Mr. D. C. Currie, Officer-in-Charge at Lephinmore Research Station, was awarded a Nuffield 'Special Interest' Travelling Scholarship and visited Australia, New Zealand and South Africa to study fat lamb and wool production. Other members of staff have visited Finland, the U.S.A., Czechoslovakia and Italy.

We have welcomed many scientists from overseas and the United Kingdom at Headquarters in Edinburgh, and the research stations have had many visitors, including parties of University, Agricultural College and Farm Institute students, and of Advisory officers and farmers.

Acknowledgments

Once again we wish to express our indebtedness to our sister research and educational institutions and in particular the Animal Breeding Research Organisation, the Animal Diseases Research Association, the Macaulay Institute for Soil Research, the Scottish Plant Breeding Station and the Edinburgh School of Agriculture.

1. HILL SOILS

M. J. S. FLOATE

Summary. A review is presented of those environmental factors which limit the potential of upland pastoral farming. In many areas severity of climate is not so great a limitation to herbage production as are deficiencies in soil fertility. Factors affecting the kind and quality of the soil resource are discussed and stress is laid upon the activity of the organic cycle of nutrients in counteracting the effects of leaching. Hill land improvement techniques involving re-seeding and manurial treatments are described and an alternative approach through a stimulated organic cycle is suggested. Some of the limitations in the soil-plant-animal cycle of nutrients are being investigated. Particular emphasis is placed upon the role of the animal in this cycle.

INTENSIVE systems of agriculture are dependent upon an environmental resource which is susceptible to a high degree of control and amendment: their potential is largely dependent upon the amount of external input. In contrast, extensive systems of agriculture are almost wholly dependent upon the environmental resource and their potential can only be achieved by the utilisation of that resource to its capacity. Knowledge of the environment therefore assumes a greater importance in, for example, such systems as upland pastoral farming. The soil environment of upland areas has, however, attracted little attention from research workers.

The chief factors of the environment affecting upland pastoral farming are soil and climate, which have a strong influence upon vegetation. The quality of the soil resource is dependent upon the soil parent material and the processes of weathering, leaching and biological activity which transform rock and glacial debris into soil. Factors which affect the kind and degree of soil development include temperature, moisture, time, relief and organisms.

The relatively high rainfall and low temperatures in the hills of Britain provide conditions of strong leaching and weak weathering. Because precipitation is greater than loss by evaporation and transpiration there is a net annual excess of moisture, which is available for leaching and waterlogging. Because of low temperatures, chemical weathering is weak and the release of bases and nutrients from most parent materials is slow. Except on the most easily weatherable and base-rich parent materials the rate of leaching is greater than the rate of release through weathering so that a net loss of bases and nutrients results (Crompton, 1958).

The losses through leaching may be minimised by an active organic cycle. Deep rooting plant species and churning organisms such as worms bring nutrients to the surface, and their return via plant litter decomposition and mineralisation keeps a considerable amount of material in circulation. A weaker organic cycle is characterised by a lower nutrient-demanding flora with a shallow root system and a population of micro-organisms capable of only slow release of nutrients from decomposing litter; as such it is less effective in counteracting leaching losses.

Soil formation conditions in the hills generally favour the accumulation of soil organic matter which is usually more or less acid. Moisture saturation, low temperatures and acidity are factors which retard organic matter decomposition and hence promote its accumulation in soil. As more organic matter accumulates, the cation exchange capacity of the soil increases and, because the release through weathering is usually insufficient to saturate the exchange sites, the result is commonly to increase the base unsaturation of the soil and lower its pH. This is frequently accompanied by a general downgrading of the soil, the encouragement of a lower nutrient-demanding flora, slower decomposition of organic matter, a weaker organic cycle, and the acceleration of leaching and/or the fixation of available nutrients through organic and inorganic reactions. Under natural conditions the downgrading process thus tends to be self-perpetuating under hill conditions, and is only counteracted by the slow release of bases from weathering, by the organic cycle, or by incremental additions of nutrients and bases in precipitation.

The development of a peaty mat and surface mor humus is characteristic of organic matter accumulation under conditions of strong leaching and weak weathering. Organic matter accumulation in these forms actively accelerates the losses through leaching; the slow breakdown of these materials releases organic compounds which are capable of mobilising certain elements and causing their removal from the profile by cheluviation faster than under normal leaching conditions by soluviation (Crompton, 1960).

The most common major soil groups of the hill areas are Brown Forest Soils, Peaty Podzols, Non-Calcareous Gleys, Peaty Gleys, Hill Peat and skeletal soils. The factors affecting the distribution of these soil groups have been discussed in general terms by Crompton (1958) and in relation to an area in the South of Scotland by Muir (1955). In general the soil surveys of England and Wales and of Scotland have concentrated on areas of intensive lowland agriculture so that only a small percentage of the total upland land surface has been mapped (Soil Survey Research Board, 1965). Nevertheless a considerable acreage of hill ground in the north-east of Scotland, south of Scotland, in northern England, and in Wales has been mapped. In view of the low intensity of research on soil problems of upland areas compared with the effort expended on lowland soils, it is important that interest should be concentrated on identifiable soil series so that the areas to which results apply may be delineated.

The climate of hill areas may be responsible for low production at high elevations. Between possible growth on every day of the year in the extreme south-west of England, and zero growing days (for plants of agricultural value) at the summit of Ben Nevis, there is the full range in length of growing season in Britain (Crompton, 1958). It might be assumed, therefore, that there should be a direct correlation between decreasing productivity and increasing severity of climate. However, Anderson and Batey (1957) found no apparent correlation between yield and altitude in northern England up to 1600 feet, and Davies (1960) has reported dry matter production of 4 tons/acre at 2250 feet in the northern Pennines from a re-seeded sward which received heavy nitrogen treatment. It is probable that for very large areas of presently low production hill land, limitations are due more to deficiencies in soil fertility (perhaps indirectly due to climate) than to severity of climate *per se*.

Most previous attempts to up-grade hill soils have involved direct injection of fertility into the soil system by fertilisers and soil amendments, frequently accompanied by cultivation and re-seeding (Stapledon, 1932; Milton and Davies, 1947; Ellison and Boyd, 1952; Anderson and Batey, 1957; Hunter, 1962). Although dramatic increases in herbage production have been reported, the widespread application of such techniques is not likely to be acceptable because of the steep and rocky nature of much of the terrain, its inaccessibility, and for economic reasons.

Alternative, and more widely applicable, methods of improvement of upland soils must therefore be sought. Such improvements are likely to be brought about by indirect methods of increasing the efficiency of the organic cycle and promoting a more rapid circulation of nutrients around the soil-plant-animal cycle.

A research programme is being undertaken to define some of the limiting factors in this cycle and to examine methods of increasing its efficiency.

The existence of vegetational and soil contrasts between the 2 sides of long-established fence-lines offers an opportunity of studying the effects of differential grazing pressure at sites where the evidence indicates development from a common origin. Sites have been selected on soils of the Ettrick, Bemersyde and Balrownie soil associations and a study of vegetational and soil changes is in progress. Under the influence of increased grazing pressure, the mineral soil profiles are associated with a larger component of *Agrostis*, *Festuca* and *Deschampsia* species and exhibit features of a higher fertility state than their adjacent counterparts under less intensive animal influence. The organic surface horizons (A_0) are usually thinner and there is commonly a mull humus horizon (A_1) which is rarely present in the less grazed member of each pair. Associated chemical changes include an increase in soil pH, a decrease in the weight of soil organic matter, and an increase in its nitrogen content which is reflected in a considerable reduction in C/N ratio of the soil organic matter. These factors affect the rate at which nutrients may be supplied to growing plants and further work is in progress on the resultant changes in the capacity and intensity factors of the nutrient supply. From the results that are available to date it appears that the long term effects of minor differences in grazing management may be to cause dramatic vegetative changes, and that improvements in soil properties result from a more active organic cycle. It may be concluded that the influence of the grazing animal on the soil-plant nutrient cycle warrants greater appreciation and study.

The effects of animals grazing the herbage and producing excreta as a modification of the sequence: plants-litter-decomposition-mineralisation are not well known and have been the subject of only a few studies. Petersen, Woodhouse and Lucas (1956) have studied the distribution of excreta by freely grazing animals and its effects on pasture fertility, and White (1960) has reported on the distribution and subsequent disappearance of sheep dung on Pennine moorlands. Barrow (1960, 1961) and Bromfield (1961), in Australia, have compared the mineralisation rates of plant material before and after passage through an animal. The results show that fresh plant material is more rapidly mineralised than faecal material. However, considerable amounts of nitrogen are released from plant material during its passage through the animal and are subsequently voided as urinary nitrogen. The balance of these effects remains to be investigated under hill conditions.

Studies are being initiated to examine the effects of introducing the animal into the plant-litter-decomposition-mineralisation sequence. The release of carbon, nitrogen and phosphorus from different kinds of plant material during incubation experiments is being compared with their release from the excreta of sheep fed on rations of similar plant materials. To date the results indicate that there are considerable differences in the amount and rate of release of ammonia -N from different kinds of plant material which comprise the natural diet of hill sheep.

Further experiments are planned to examine the effects of increasing sheep grazing density and of increasing levels of dung and urine application on parameters of soil nutrient supply and on the activity of the organic cycle in upland soils. Other factors of probable limitation to the efficiency of the organic cycle which are being investigated include acidity and related soil properties.

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2. HILL PASTURES

J. KING, SHEILA A. GRANT AND J. A. ROGERS

Summary. Hill pasture vegetation is discussed in relation to grazing pressure in the context of the present farming system. Distinction is made between desirable and undesirable changes in the composition of indigenous pasture and the factors which bring these about. The manipulation of pasture composition by chemical means is possible but of limited value at present. The introduction of more productive species is desirable but pasture composition will be determined ultimately by environmental factors. Reference is made to the potentialities of poorly drained sites on gleyed soils. Climatic limitations to plant growth are discussed in terms of effects of light and temperature on growth in spring and of climatic changes associated with altitude on sward production.

IN a grazing system where overall stocking rate is fixed, and where the animals have free access to a variety of vegetation types, each type tends to support a characteristic seasonal pattern and intensity of grazing. This in turn affects both vegetation and soil, giving rise to a soil/vegetation/grazing complex in which the component parts are highly interdependent. This is the situation which prevails on hill land at the present day. The resultant pastures and their associated soils appear on the whole to be remarkably stable, although still subject to slow changes and not completely in equilibrium. This soil/vegetation/grazing complex, especially as it relates to grassland and heather, has been the subject of a number of studies by workers in the Organisation. The relationship between vegetation pattern, seasonal grazing pressure and social behaviour of sheep has been studied by Hunter and others (Hunter, 1962 *a*, *b*; Hunter and Davies, 1963; Hunter and Milner, 1963). Much of this information, together with data on soil type/vegetation relationships and the published results of other workers has been summarised in the chapter on forest zone grasslands in *The Vegetation of Scotland* (King and Nicholson, 1964). From this and other relevant chapters in this book it is apparent that a good deal is known about the composition of existing hill pasture types and their broad relationships with major environmental variations. Certainly it is possible to identify and classify most if not all pastoral plant communities on hill land in Scotland and so to provide a frame of reference for other work.

All this information is, strictly speaking, only applicable within the context of the traditional hill farming system based on uncontrolled sheep grazing. It is a description of the existing situation which must be changed if the potential of hill land is to be realised. This will require control and manipulation not only of grazing, but also of pasture composition and soil conditions. To this latter end much of the present botanical work is directed.

For this purpose it is convenient to think of the environment separately from the vegetation and to describe the former in terms of small site-units, roughly comparable in scale to plant communities. Such site-units are defined in terms of physical factors affecting plant growth, such as temperature, wind exposure, etc., or more loosely in terms of complexes of factors such as altitude, aspect, soil parent material or profile type and so on. They can be classified into a comparatively small number of site-types. According to this concept each site-type can support any of a range of vegetation types, the one actually occupying a given site depending on the species available and on animal or human factors (mainly grazing pressure and associated practices such as burning). Assuming that only existing hill species are available, and excluding both land covered by deep peat and land above 2000 feet, the vegetation can be expected to vary with the grazing/burning pressure very broadly as shown in Figure 1. This

FIG. 1

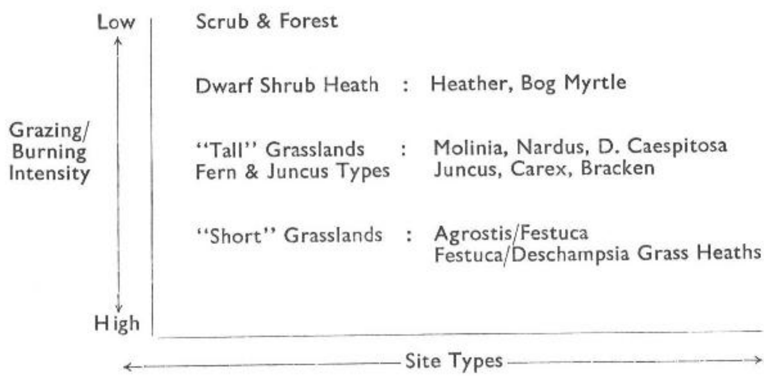

diagram can be taken to imply that on most site-types the different categories, short grassland, tall grasslands, etc., and shrub heath, are interchangeable and that, by suitable manipulation of the grazing, the vegetation can be changed to suit the nutritional demands of the grazing animal. Some of these changes have already occurred as a result of the existing grazing system, but mainly in the direction of the more unpalatable tall grass types, such as *Nardus* or *Molinia* pastures or bracken. Such undesirable changes, particularly those in which *Nardus* or *Molinia* is involved, have been the subject of investigation (King, 1960, 1962; Grant *et al.*, 1963) and the position of these species in relation to various plant communities is probably as well understood as it can be on the basis of survey data. Further advances will depend on an experimental approach.

Another undesirable effect that has been thought to take place under the present grazing system is the loss of nutrients from heather communities after they have been burned. This has been the subject of investigations jointly carried out with the Macaulay Institute (Robertson and Davies, 1965). From these and from data of Allen (1964) it appears that the most serious loss is of nitrogen, most of which takes place in the smoke. Other nutrients are also lost, but on many soils the loss is minimised by the ability of the soil to absorb nutrients and on most it is balanced by the nutrients supplied naturally in rainfall. Under some circumstances however, or on soils of low absorptive capacity, this may not be sufficient and appreciable losses might then occur over a period of years. Losses due to sales of livestock are extremely low in comparison with the potential losses from burning.

The emphasis in all this work has been on undesirable changes in the vegetation or soil conditions. In contrast comparatively little attention has been paid to potentially desirable changes, particularly those associated with high grazing pressures leading to short grass types (Fig. 1). As a group the indigenous short-grass communities appear to have a greater potential than the taller communities. The latter, under free grazing, support much lower comparative grazing intensities (Hunter, 1962*a*) and this may be due to the unpalatable nature of most of the taller species. So far this can only be an hypothesis, as the data available do not permit a separation of the effects of various soil conditions and the presence or absence of the species in question. If the hypothesis is correct and the short grassland types also prove to be more productive under controlled grazing conditions, then a great deal of pasture improvement will be possible by eliminating the taller species and increasing the area of short grassland. This latter is at present made up of various *Agrostis/Festuca* communities, ranging from those dominated by *Agrostis tenuis*, *Festuca rubra* and white clover to the grass-heaths in which *Festuca ovina* and *Deschampsia flexuosa* predominate. These communities appear to lend themselves to utilisation in different seasons (see Section 4), and so may form a reasonable basis for a system of controlled grazing. It must be remembered however that on many site-types short-grass communities do not at present exist. Nothing is known therefore of their compositional stability on these sites and it is probable that on some they will prove difficult to maintain. If this is the case, alternative communities can be sought, either by encouraging dwarf shrub heath or by introducing tall or short grass species of lowland origin, after suitable modification of the site by fertilisation or drainage.

Considering the possibilities of pasture improvement as a whole, there seem to be three possible lines of approach which are likely to be compatible with animal requirements. These are: (1) To produce or maintain dwarf shrub heath without site modification. (2) To produce indigenous short-grass communities maintained by high grazing pressure, without modification of the site. If the site is modified by fertilisation there is the further possibility of increasing the area of *A. tenuis/F. rubra* grassland at the expense of the *F. ovina*-rich communities. (3) To introduce lowland species, which may be tall or short in habit, accompanied by some modification of the site.

Only a small amount of work has been carried out on the possibility of maintaining a productive shrub heath. The effect of defoliating heather by clipping has been studied by Grant and Hunter (1966) and the results suggest that the optimum grazing intensity would be one which removed about 60% of the current season's growth. This corresponds to a fairly high grazing pressure and would tend to keep the community short, dense and physiologically young. It is possible that heather managed on these lines would not only maintain a high level of production and nutritional value, but also would very rarely require burning. Studies of grazing and burning effects on heather show that grazing does in fact increase the nutritive value of the current season's growth (Grant and Hunter, 1966) and may also lead to earlier spring growth. However, it may delay re-establishment after burning, and it is well known that heavy grazing frequently produces a change from heather to grassland. This might make it difficult in practice to manage heather in this way, but on certain soils at least it should not prove impossible to devise a suitable grazing management.

Experiments with selective herbicides have been carried out in the past (King and Davies, 1963) and it is clear that these will have a useful part to play in the manipulation of pasture composition. As an example, both *Nardus* and *Molinia* are susceptible to low rates of application of Dalapon, to which the short-grass species *F. ovina* and *D. flexuosa* are relatively resistant. On the communities where these occur together it is therefore possible to convert these pasture types to short *Festuca-Deschampsia* grassland with some desirable attributes. Combined with increased grazing pressure this might eventually find a place in farm practice. However, with the existing uncontrolled system of grazing there seems to be no reason to expect that an increase in the area of this particular short-grass type would necessarily result in any increase in animal production, nor is there much known about the long-term stability of the new community. The best use of chemical sprays will be as part of a system of grazing designed to make use of the resultant changes, but this stage has not yet been reached. It must also be remembered that many species such as *Holcus* and *Carex* spp. are resistant even to heavy applications of herbicide, so that there is serious risk on some communities of producing a pasture in which one species is undesirably abundant. There is a need for new herbicides capable of killing these resistant species and at the same time reducing the cost per acre to a level where application rates sufficient to effect a complete kill become economic.

Although chemical sprays provide a rapid means of changing pasture composition, the long-term effect will be dependent on grazing management, soil fertility and the soil moisture/aeration regime. In this connection the effect of defoliation on the behaviour of a number of hill species has been studied both on spaced plants (H.F.R.O. 3rd Report pp. 49-51) and on 50/50 mixes of pairs of species. Amongst other things, this work has shown that species differ in their sensitivity to defoliation, some giving greatly reduced yields in the following spring as a result of defoliation in October, others being less affected. When applied to mixtures of two species in swards this results in a tendency for the insensitive species to increase at the expense of the sensitive species.

A study of the effect of fertility level on the balance between *F. rubra* and *A. tenuis* in a sward has shown that at the high fertility levels *Festuca* increases its contribution to a mixture of these species at the expense of *Agrostis*, while at a lower level neither species suppresses the other. This result appears to be due in part to competition for light. The taller *Festuca* under fertile conditions is able to intercept most of the light while at a lower fertility level its growth is shorter and less dense, enabling the more prostrate *Agrostis* to receive sufficient light for growth. The increased percentage cover of *F. rubra* at soil pH levels greater than 5·2 (Fig. 2) suggests that this fertility effect may occur in the field, despite the relatively high grazing pressure associated with communities on such mesotrophic soils. However, the field situation is complicated by the presence in abundance of other species, *F. ovina* in particular, and more work will be necessary to identify all the factors influencing the composition of these pastures.

Introduction of New Pasture Species—Effect of Soil Type

All this presupposes that only the existing hill species are available and that no modifications are made to the site-type. Plainly, there would be great potentialities if sites could be modified and grazing controlled to permit the introduction of more productive species. These might be of hill or of lowland origin. The aim would be to produce plant communities related to, but more productive than, the existing ones, adapted to the modified environment and stable in their composition.

This leads directly to a consideration of the differences between site-types and the response of individual species to them.

The site-type can be defined in terms ranging from major environmental components to individual factors (Table 1). At present no

TABLE 1

Major components	Site complexes	Factors
(*a*) Soil profile type (integrating all previous site history and parent material effects)	Soil moisture regime Soil nutrient level	e.g.: soil O_2 or CO_2 levels soil chemical characteristics etc.
(*b*) Climate (*c*) Topography	Site microclimate	e.g.: temperature, rainfall, evaporation, wind speed etc.

adequate site-type classification exists for hill land, the nearest approach being the descriptive accounts of vegetation and environment already referred to in the *Vegetation of Scotland*. In this account the grassland communities have been arranged in relation to two axes of environmental variation, soil moisture/aeration regime and soil base status. The nature of the floristic variation associated with these environmental complexes is shown by the data used to construct Figure 2. These allow the percentage cover of individual species to be 'mapped' in relation to the environmental axes using integrated soil moisture tension to provide an index of the moisture/aeration regime. Superimposition of these and other species diagrams provides a composite picture of the vegetation which forms the starting point of any scheme of pasture improvement. The first requirement for the development of improved plant communities is to obtain data on the growth of individual species in the absence of competition, both under controlled conditions at the site-complex level and also under conditions where the effects of individual factors can be measured. The response of species to water-logging, and the factors associated with it, is of particular interest and is at present the object of investigation. In Figure 2 the soils below 40 on the moisture/aeration axis are to some extent anaerobic in the surface horizons throughout the

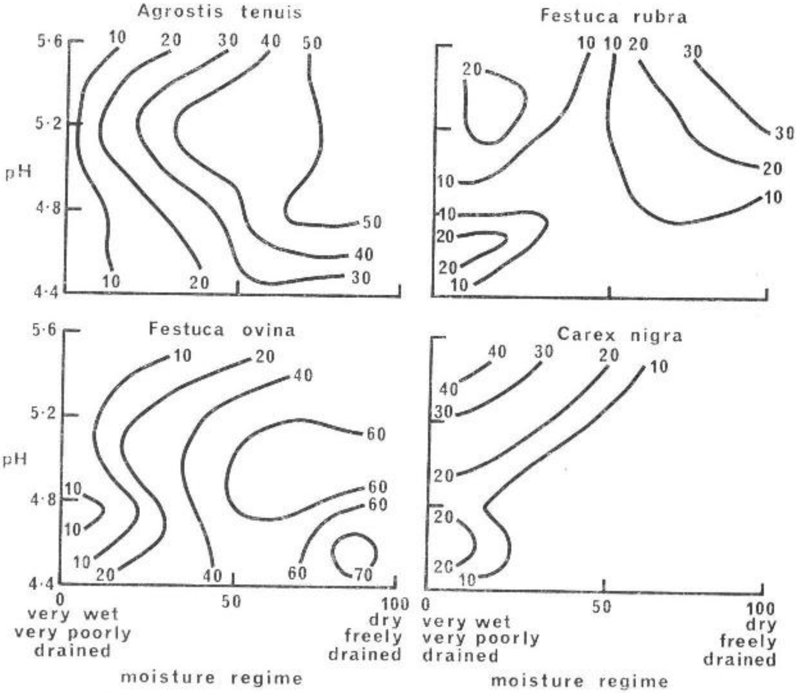

FIG. 2. Percentage ground cover of species in relation to soil pH and moisture/aeration regime.

year. Oxygen is low, carbon dioxide is high, toxic levels of sulphides may be produced and changes to plant nutrients may either render them more available or available in such quantities as to be toxic. Yields of herbage and especially root growth are undoubtedly reduced by anaerobic conditions. However, there appears to be some interspecific variation in this respect and data so far available suggest that it may be possible to introduce into anaerobic sites species which are more tolerant of the conditions and apparently more productive than the existing species. Tall fescue is the most promising species so far examined. This possibility is attractive because not only are wet anaerobic soils widespread in hill areas, but also because a great many of the more mesotrophic and potentially fertile hill soils belong to this category. These are usually surface-water gleys difficult to drain and whose production potential will only be realised by the use of suitable species adapted to, or at least tolerant of, such conditions.

Effects of Light and Temperature

In addition to the effects of soil factors, climate also influences plant growth. Individual climatic factors must clearly be examined, and in particular those which normally tend to vary together and whose effects are impossible to separate under field conditions. Light and temperature are one example, both factors increasing and decreasing together especially during spring and autumn. Dry matter accumulation is affected both by efficiency of the leaves in intercepting and converting solar energy and by the rate of formation of the organs of light interception, i.e. rate of foliage production. The measure of the first component is given by the net assimilation rate, while the second is a compound of rate of leaf expansion, rate of leaf production and rate of tillering.

Experiments are in progress in which the relationships of each of these parameters with temperature and light are being measured. Early indications are that, where foliage production is concerned, temperature would appear to be the main variable controlling leaf extension growth, light having little or no effect. Rate of leaf appearance is mainly controlled by temperature, but the relationship is somewhat looser and there are indications that light may also be of some importance. With rate of tillering however, light and temperature interact so that correlations between tillering rates and temperature are low.

These results suggest that an order of priority exists whereby energy supplied by the products of assimilation is first used up in the growth of existing tissues (cell expansion), secondly at primary apices (cell initiation and cell expansion) where new leaves are being produced, and thirdly at secondary (axillary) growing points where new tillers are formed. During periods of low light intensity, when assimilation is slow, insufficient assimilate is available for the last stage and tiller development is affected. If these tentative conclusions are confirmed it would appear that, in a sward where tiller density was already reasonably high, and further tillering therefore limited, temperature rather than light will be the most important factor influencing the rate of foliage production in early spring and late autumn.

The effect on plant growth of climatic variations associated with topography, and particularly with altitude, are of interest especially if they enable generalisations to be made about site differences. Such studies have been carried out using S 23 ryegrass and swards of indigenous *F. rubra* grown alone and in mixture with S 184 white clover. South-facing slopes were used, ranging mainly from 750 feet to 1750 feet, but in some cases to over 2000 feet. Soil conditions were constant at all altitudes. The results confirm that not only does herbage production vary with altitude, but that the greatest overall production may be obtained at intermediate levels of 1000 to 1250 feet. Taking the results for *F. rubra* and white clover for two complete seasons, total dry matter yields expressed on a relative basis varied as shown in Table 2. Four main factors are involved. Three of

TABLE 2

Relative Total Season's Yield at Different Altitudes

Altitude	S 184/*F. rubra*	*F. rubra* High N	*F. rubra* Low N
750 ft	80	85	86
1000–1250	100	100	100
1500	81	85	75
1750	67	84	71

these, temperature, rainfall, and wind speed, increase with altitude, and one, evaporation, decreases. In this study moisture deficits occurred regularly at the lowest altitude, but rarely at higher elevations. The relative importance of these factors varied as the season advanced so that the optimum altitude for plant growth also varied seasonally. In spring, growth tended to be greatest at the lower levels, decreasing in a linear manner with increasing altitude. Generally speaking, the yield at 750 feet at the end of May was about twice that at 1750 feet, the difference tending to be greater for the clover sward and rather less for *F. rubra* growing at a low nitrogen level. This variation with altitude was correlated with trends in temperature and wind speed.

During June, differences between altitudes were either absent altogether or were much smaller than in spring. The form of the yield/altitude relationship was also variable, being either linear or quadratic. From July onwards the highest yields were commonly obtained at intermediate altitudes (i.e. 1000 feet-1250 feet), the yield/altitude relationship generally being quadratic. Dry matter yields at the lowest elevation at this time of year were 20 to 50% less than those obtained at 1000 or 1250 feet. At 1750 feet they were from 10 to 25% less for *F. rubra* and up to 45% less for the clover sward. The yield depression at low altitudes is related to moisture deficits, while that at high altitude is associated with high wind speeds and lower temperatures. The relative importance of these last two factors in this situation is not yet known.

These generalisations must be modified for particular sites where conditions differ markedly from those in the experiments. For this, data on individual factor effects and interactions will be needed. In the Cheviot region, moisture deficits sufficient to reduce plant growth to a significant extent seem to occur regularly at 750 feet, at least on southerly slopes. Further west in regions of greater water surplus and possibly also in the east on steep north-facing slopes, deficits will be smaller and the zone of optimum production might be expected to extend downwards to below 750 feet. There is evidence that soil fertility level may sometimes interact with altitude in such a way that climatic effects are minimised. At very low fertility levels, therefore, responses to climate may prove to be smaller than at higher levels.

Interactions with soil drainage conditions must also occur although data are lacking on this. Presumably, wet sites on gleyed soils will not suffer from moisture deficits at low altitudes, but may on the other hand be affected by increased water-logging at higher altitudes. In general the evidence so far available suggests that the climate prevailing on hill land at altitudes up to 1250 feet is not likely to limit spring and summer herbage production to a significant extent, although in spring the earliest growth will always be obtained at the lowest elevations.

Since moisture shortages frequently limit summer growth at lower elevations, production at this season will often be greatest at intermediate altitudes. Above 1500 feet yields are relatively low at all times in the growing season.

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3. THE DIGESTIBILITY OF INDIGENOUS HILL PASTURE SPECIES

J. S. BLACK

Summary. The digestibility of hill pasture species has been examined at different times of year under different cutting regimes. The rate of decline of digestibility in uncut plants is related to date of flowering; early-flowering species such as *D. flexuosa* and *F. rubra* show a more rapid decline than later-flowering species such as *A. tenuis* and *H. mollis*. Cutting at intervals of not more than 6 weeks allows maintenance of high digestibility values throughout summer and autumn. Fine-leaved species maintained higher values during winter than broad-leaved species.

THE digestibility of a forage is a useful index of its nutritive value. But under hill pasture conditions the determination of such a value by conventional means for individual species is virtually impossible as single species swards do not exist. A few investigations have attempted to determine digestibility *in vivo* of native hill pasture species using material harvested from pastures where the species under study constitute a high proportion of the sward, e.g. *Nardus stricta* (Thomas and Fairbairn, 1957) and *Molinia coerulea* (Thomas and Ibbotson, 1947). Because of the difficulties involved in collecting material, few determinations were possible. However, with reliable *in vitro* methods of determining digestibility now available, it is possible to study in greater detail the digestibility of individual species under a range of conditions.

From small plot experiments, using transplant material grown in an unfertilised brown earth soil, it would appear that digestibility is controlled by attributes of the individual species in three distinct periods of the growth cycle: (1) in growth to maturity, (2) in regrowth after cutting, (3) in the period of senescence during winter. Four hill species were used in all trials, viz., *Agrostis tenuis*, *Holcus mollis*, *Festuca rubra* and *Deschampsia flexuosa*. At the same time attempts were made to grow *Lolium perenne* (S 23) in the same environment to give a comparison of the hill species with the best-known lowland counterpart.

Growth to Maturity

As the plant grows to maturity dry matter (D.M.) production increases, but digestibility, initially high, declines. The speed of decline is related to the date of flowering. Table 1 summarises the data available for the four hill species over a 3-year period. *L. perenne* (S 23) data are available only for 1 year. The species are divided into groups according to date of flowering.

TABLE 1

Growth to Maturity

Species	Date of 50% ear emergence	D.M. digestibility % (*in vitro*) Mid-May	Early June	Late June
D. flexuosa and *F. rubra*	25th May-2nd June	75	68	57
H. mollis and *A. tenuis*	21st June-6th July	76	72	62
L. perenne (S 23)	21st June	78	81	67

In mid-May, when only *D. flexuosa* and *F. rubra* had produced stem material, there was very little difference between the species in digestibility. In some years the digestibility of *F. rubra* was significantly lower than that of *D. flexuosa* and *H. mollis*, but this occurred when the times of sampling and ear emergence were close. All species except *L. perenne* (S 23) declined in digestibility from the first sampling date in mid-May, but the steepest fall occurred in the early-flowering species.

The pattern of decline in digestibility of these hill species is very similar to that reported for some lowland species (Minson *et al.*, 1964). The figures for *L. perenne* (S 23) are very similar to those recorded by Minson *et al.*, (1961). The main difference in all cases is related to the date of 50% ear emergence, which is very much later under hill conditions. Such differences are to be expected because of the higher altitude and latitude of Sourhope (900 feet above sea level) in South Scotland compared with the Grassland Research Institute in Southern England (Cooper, 1952). It can thus be concluded that the hill grasses have a potential digestibility in early spring which is very similar to that of lowland species, with the possible exception of some ryegrass strains, and that the changes in digestibility are functions of the change in proportions of leaf, leaf sheath and stem (Terry and Tilley, 1964).

Under pasture conditions frequent defoliation will be required in this phase to keep the pasture in a highly nutritious state. This is particularly true if a pasture has two co-dominants with widely spaced flowering dates, e.g., *Agrostis-Festuca* pasture containing *A. tenuis* and *F. rubra*.

Regrowth Period

Regrowth of the four hill species was largely composed of leaf material; the only exception was in the regrowth period following the first defoliation just after the point of 50% ear emergence, when elongation of decapitated stems occurred. It is thus not surprising that regrowth digestibility values during summer and autumn tended to remain constant, with a slight increase in autumn. However, in 1 year out of 3, a midsummer depression occurred in the broad-leaved species *A. tenuis*, *H. mollis* and *L. perenne* (S 23). Regardless of the length of the regrowth period, the differences in digestibility values between the five species tended to persist. *L. perenne* (S 23), *D. flexuosa* and *H. mollis* generally showed the highest values. *A. tenuis* was always lowest, with *F. rubra* occupying an intermediate position.

The length of the regrowth period had a considerable effect on digestibility. Table 2 gives values for 3, 6 and 15 weeks after defoliation in early June. *D. flexuosa*, *F. rubra* and *H. mollis* were similar in their reaction to the length of the regrowth period; values were similar in 3- and 6-week regrowths. *A. tenuis* on the other hand declined in digestibility before the end of the 6-week period.

In practice the length of the regrowth period will have to accommodate not only the species decline in digestibility but also the possibility of a summer depression, which will also be accompanied by a reduced total D.M. production.

TABLE 2

Effect of Length of Regrowth Period on % D.M. Digestibility

	Length of regrowth period		
	3 weeks	6 weeks	15 weeks
D. flexuosa	73	72	62
A. tenuis	67	64	56

Winter

Digestibility changes were followed during winter in material conserved *in situ* from August. Values in late October are a resultant of the length of the regrowth period, the autumn rise in digestibility, and the climatic variations in September and October. But high values were generally obtained. By December however, in the two winters (1962-63 and 1965-66) when this work was carried out, digestibility had fallen to a lower value; the rate of fall was very similar in both years and for each species. In the severe winter of 1962-63 digestibility continued to fall until March. In the mild winter of 1965-66 no fall was observed between December and March, except in *A. tenuis*.

The overall change in digestibility between late October and March in the two years is summarised in Table 3. The fine-leaved species *D. flexuosa* and *F. rubra* maintained higher values in both winters than did the broad-leaved species *H. mollis* and *A. tenuis*. *A. tenuis* declined in digestibility to around 40% regardless of winter conditions. The response of *L. perenne* (S 23) is more difficult to evaluate as it died completely in 1962-63.

TABLE 3

% D.M. Digestibility in Autumn and Winter

	1962–63		1965–66	
	Oct.	March	Oct.	March
D. flexuosa	77	62	77	69
F. rubra	73	48	72	63
L. perenne (S 23)	74	43*	77	62
H. mollis	73	42	69	53
A. tenuis	70	35	64	41

* S 23 died in the 1962–63 winter.

In 1962-63 a high negative correlation was obtained between digestibility values of the individual species in March and the D.M. previously available in late October. In 1965-66 no correlation was obtained.

Conclusion

Hill pastures have a high potential to produce, when required, a forage of high nutritive value. It must be emphasised that the data in the preceeding discussion cannot be transferred directly to a pastoral situation, but broad conclusions can be drawn. All species can provide forage material with a high digestibility in early spring. These high values can be maintained only if flowering is prevented. Subsequent regrowth, conserved over not more than 6 weeks, will provide a relatively constant level of digestibility throughout summer and autumn. Winter digestibility values will be highest in regrowth conserved from August in the form of pasture containing a high percentage of fine-leaved species.

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4. THE NUTRITION OF GRAZING HILL SHEEP; UTILISATION OF HILL PASTURES

J. EADIE

Summary. Year-long set-stocking of hill pastures creates a vicious circle, in terms of nutrition and hence production. The amount of herbage consumed is small in relation to what is produced during the period of active growth. Selective grazing buffers the animal against a rapid fall in the quality of the diet during summer, but the system creates a large carryover of mature herbage which dilutes the quality of the feed available in the critical spring-early summer period. The annual cycle of nutrition is therefore to a large extent a result of the management system, and does not reflect the capacity of hill pastures to produce high quality feed. The problem of breaking through the nutritional limitations of set-stocked pastures is discussed in the light of experiments which illustrate the potential of these pastures and the adverse effects of accumulated dead herbage. The essentiality of control of grazing is emphasized.

HILL pasture improvement has generally come to mean hill soils improvement accompanied by the replacement of existing hill vegetation by lowland-type pasture. A range of techniques is now available for a wide variety of hill environments. But this kind of improvement is expensive and is often economically marginal in its effect, and the problem of the integration of such improved areas to the benefit of the overall utilisation of hill pastures has never been satisfactorily solved. The assumption behind these procedures is that hill vegetation is inferior in some respect or respects and this assumption requires closer examination.

Nutrient Intake under Extensive Grazing

The rational use of improved areas and the deficiencies of hill vegetation are clearly questions whose answers contain an important nutritional component. The impact of vegetation on sheep production and performance is largely nutritional, and in order to shed some light on an area hitherto subject to much guesswork a study of the annual cycle of nutrient intake of sheep on an area typical of the Eastern Cheviots was undertaken at Sourhope during the years 1961-64.

Maximum energy intakes occur in the May-June period, but are moderate compared to those attained on reasonably well-managed lowland grassland (maximum around 65 g. D.O.M./kg.$^{0\cdot73}$). The decline during the summer is relatively slow, but from late autumn to late winter sub-maintenance nutrition levels are the rule (range 18-35 g. D.O.M./kg.$^{0\cdot73}$). Energy intakes improve in late winter-early spring, over the period coincident with the latter part of pregnancy, but this improvement varies considerably from season to season. This variation is a consequence of the ingestion of varying proportions of new season's growth and is closely related to soil temperatures.

The energy intake cycle is largely determined by the quality of the herbage ingested during the year, and the relationship between energy intake and digestibility is partly dependent on the fact that there is a positive correlation between voluntary intake and digestibility.

Maximum digestibility values of the ingested herbage are around 75 and occur in May and June. They fall to 70 by mid-July and decline rapidly at the end of the pasture growing season, approaching 50 by December and reaching 48 in February. Between-year differences in digestibility are small except for the late winter-early spring period (Fig. 1).

Systems of hill pasture management are usually set-stocked, year-long systems. Hill pasture growth, on the other hand, is highly seasonal. The result is that over the period of active pasture growth the amount of herbage consumed by the sheep is small in relation to what is produced. Thus the sheep are able to graze selectively and maintain the quality of their diet. But the uneaten herbage, a large proportion of the total production, accumulates and matures and so dilutes the quality of the available feed. Although in winter the death and decay of plant material together with grazing reduce its quantity, there is a considerable carryover of dead mature herbage from one season to the next.

It has already been pointed out that the quality of the herbage eaten is at its best in early summer, but even then it is only moderate by lowland standards, and recent work has shown the importance of dead herbage in limiting the quality of the sheep's diet.

Current hill pasture management systems therefore create a vicious circle. Stocking rates, set at levels determined by the need to maintain a certain minimum level of winter nutrition, permit the sheep to graze selectively. This buffers the animal against a rapid fall in the quality of the diet during summer, but also creates a fund of mature herbage which sets a relatively low ceiling on diet quality in early summer.

The annual cycle of nutrition is therefore to a large extent a function of the management system, and does not reflect the capacity of hill pastures to produce high quality feed.

The relation of the nutrition cycle to animal performance shows that the marked between-year differences in pre-partum nutrition do not result in significant differences in the birth-weights of single lambs, although small differences do occur in twins. Nor are they reflected in the growth rates of single lambs. At 230 g. (0·5 lb.)/day from birth to marking, these are very similar from year to year. This growth rate, together with the fact that those of twins are so poor as

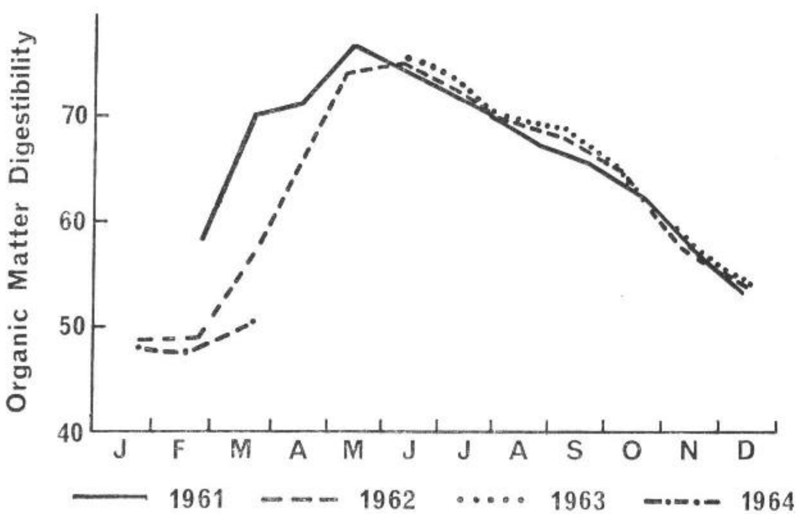

FIG. 1. Seasonal changes in digestibility of pasture consumed by sheep set-stocked on a Cheviot hill

often to necessitate removal from the hill altogether, shows that the nutrition of nursing ewes is quite inadequate to exploit the potential of the hill lamb for growth. Birth to weaning growth rates of about 180 g. (0·4 lb.)/head/day, when compared to birth to marking gains, indicate a marked falling off as grass replaces milk in the lamb's diet (Section 8). A declining level of nutrition from the end of lactation restricts accumulation of the body reserves needed by the ewe for winter maintenance. Tupping takes place over a period of sub-maintenance and declining nutrition and the moderate levels of reproductive performance, again well below potential (Section 6), probably reflect not only nutrition at this time, but the overall inadequacy of the nutrition cycle.

Nutrient Intake during Lactation

It is clear that nutrition during lactation is of substantial importance, and that many of the objectives of hill pasture improvement will depend upon what it is possible to achieve during this period.

Over a period of two years, some 40 ewes which had been fairly severely undernourished during late pregnancy were given access at the beginning of lactation to either a hill sward containing a high proportion of over-wintered dead herbage, or to an area reseeded some years before. On the former the digestibility of the herbage eaten declined from around 75 to 70 over a 9-week period, which quite accurately reproduced the nutritional conditions over the same period on the open hill. Digestibility values on the reseeded area were maintained some 4 to 5 units higher over the same period.

The milk yields and lamb growth rates are summarised in Table 1. The wide ranges in each group reflect in part the very variable intakes of the ewes on each pasture, and this variation is currently being investigated.

TABLE 1

Milk Yield and Lamb Growth Rate
(9-week means; g. per day)

		Hill pasture	Reseeded pasture
	Milk yield	930	1110
Singles	Lamb growth rate (aver.)	213	258
	Lamb growth rate (range)	186–268	204–326
	Milk yield	1010	1775
Twins	Lamb growth rate (aver.)	154	218
	Lamb growth rate (range)	114–172	204–245

The major response to improved nutrition in single-bearing ewes was in terms of ewe body weight increase, but an improvement in milk yield leading to better lamb growth rate was also obtained. The limited evidence available for twin-bearing ewes suggests that a similar nutritional improvement during lactation almost doubles milk yields. The effect of the difference in nutrition levels is seen as the difference between failure and ability to satisfactorily nourish and grow twin lambs.

It is worth noting that better lamb growth was not achieved at the expense of ewe body condition, and that invariably the better nourished ewes, although producing more milk, were in superior body condition at the end of the observations.

However, unless the improvement in pasture conditions is maintained, much of the early advantage will be lost (Section 8). Thus the improvement of ewe nutrition during lactation creates a need for a similar improvement when grass becomes an important element in the lamb's diet. In addition, the capacity to satisfactorily nourish twin lambs, and the more efficient use to which twin-bearing ewes put improved nutrition, creates an interest in the promotion of twinning, and consequently in improved nutrition in autumn and early winter (Section 6).

It is impossible to escape the conclusion that sheep performance is a function of the overall nutrition cycle. Existing lamb growth rates, low fertility, too many barren ewes, and high lamb losses at birth are all in part an indication that for too much of the time nutrition is inadequate. It follows from this that improvements in nutrition at what might be thought to be critical periods cannot be expected to yield more than marginal benefits. What is clearly required is a general overall improvement in the cycle.

The proportion of the herbage produced by hill pastures which is actually eaten by sheep is less than 30%, and although low efficiencies of use are to a certain extent inevitable in year-long pasture systems there is nevertheless much room for improvement.

To some extent the nutritional deficiencies of any pastoral system can be partly eliminated by the use of supplementary feed. Such supplements may well prove to be necessary in any event. But this possibility must not be allowed to obscure the real issue, which is to evolve systems of management which will effectively harness the potential of the hills and yield a nutritional background consonant with improved animal performance and output.

From the analysis made earlier in this paper the vicious circle which lies at the root of the problem has to be broken, and it is difficult to see how this can be done within the context of free-grazing systems. A degree of grazing control is essential. The nutritional objectives have been outlined; what now must be considered is what is necessary for their achievement.

Improved Utilisation of Hill Pastures

Recent work has begun to illuminate the possibilities which flow from the capacity to control grazing. We can crudely classify hill pastures into two major categories on the basis of existing vegetation, productivity and soil potential. The more productive *Agrostis-Festuca* pastures provide the best starting point for intensive summer use. We have also begun investigations to seek means whereby the winter carrying capacity and nutritional possibilities of those areas currently dominated by *Nardus* and *Molinia* may be improved. This is not to suggest that the improvement which may follow soil amelioration and grazing control in this latter category of pastures (Section 5) is to be ignored. The approach merely recognises the fact that we start from an existing situation.

Reference has already been made to the importance of dead herbage in diluting the quality of the diet of the grazing sheep in early summer. Full utilisation in May, June and July of the primary production of *Agrostis-Festuca* pastures, when some 900 kg./acre dead herbage is present, has been shown to incur a nutritional penalty relative to existing nutrition levels on the open hill over the same period. Stocking rates incurring no nutritional penalty lead to an accumulation of the primary production and hence do not break the 'vicious circle' previously referred to. But a reduction of the dead herbage to some 250 kg./acre allows full utilisation and high quality intakes to be combined (Table 2). Full utilisation is more than a desirable end in itself; it is necessary to avoid neglected herbage creating problems at subsequent grazings.

TABLE 2

Effect of Accumulated Dead Herbage on Quality and Quantity of D.O.M. Intake

Dead herbage kg D.M./acre	Stocking rate (per acre)	D.O.M. utilised (kg/acre)	D.O.M. intake (g/head/day)
900	3	260	1135
	5	370	930
	7·5	520	815
245	6	525	1155

That *Agrostis-Festuca* pastures can yield high quality intakes is no longer in doubt. The problem now is to find ways in which the existing fund of dead herbage can be reduced at least cost in terms of individual animal nutrition, and at greatest speed. Several possibilities are currently being investigated.

The need to improve nutrition in late autumn and early winter has already been indicated. By resting previously grazed *Agrostis-Festuca* grassland during August, September and October it is possible to attain a feed quality during November-December much superior to that currently obtained and so replace a sub-maintenance diet with a supra-maintenance diet. Not only will this provide a flushing effect at tupping, but it will also make an important contribution to winter nutrition by markedly reducing the period over which body reserves are drawn upon.

One of the important consequences of the controlled management of *Agrostis-Festuca* pastures in summer is that the growth conserved into late autumn and winter is unlikely to be very winter hardy. There seems little point in conserving it for use much later than the end of the year.

It is therefore necessary to think of a year-long pastoral system based on a two-pasture concept. The *Agrostis-Festuca* areas will provide the bulk of the summer grazing, providing much better nutrition than that currently obtainable, and will be fully utilised. But it is necessary to look elsewhere for the winter food supply.

Some preliminary work has begun on the assessment of the possibilities of the *Nardus*- and *Molinia*-dominant areas as sources of winter feed. The existing fund of winter-green herbage has been shown to be of the order of 400-500 kg./D.M./acre, and there is some evidence that the species contributing importantly to this fund are much less liable to deteriorate in feeding value than many others. But this fund currently exists in company with three to four times its own weight of dead herbage to which the main contributors are the existing dominants, *Nardus* and *Molinia*. The presence of this amount of dead herbage is clearly important in determining the quality of the herbage sheep are able to extract from such pastures.

Various 'improvement' possibilities suggest themselves. The effect of reducing the fund of associated dead material must be looked at. Grazing pressure (or herbicides) will fairly easily remove the dominant species. Will this improve the contribution of the desirable winter-hardy species to the fund of green material? What is possible here will determine in large measure the approach to these poorer hill swards. 'Improvement' could mean two quite different things. Such areas could well make a much more important contribution to a pastoral system as sources of winter feed by means of much less radical vegetational changes than they would through more conventional improvement procedures.

In conclusion, it would be naïve to suppose that there is one generally applicable answer to the production problems of hill farming. What is abundantly clear is that any effective solution must deal with the basic nutritional problem, and it is likely that this is similar in nature, though it may vary in degree, throughout the range of hill land productivity. It is equally clear that solutions must in the main be based on the pastoral resource. The analysis of the pastoral problem given here is based on evidence obtained from a predominantly grassy hill area, but the conclusions are widely applicable, certainly throughout the better hill areas.

The implications of the argument advanced here are far reaching. The suggestion is not that renovation and reseeding have no place, but rather that they ought to be regarded as possible secondary, rather than the initiating, phases in an improvement programme. Lower down the hill land productivity scale it may well be necessary to 'kick off' an improvement sequence with the aid of a measure of conventional grassland improvement. But here again a rational integration of such improvement requires grazing control.

The work carried out so far has necessarily been on a small scale. But it seems sufficiently promising to be worth attempting a large-scale development exercise, since only within a whole and continuing system will it be possible to assess the extent to which this approach makes a real contribution to the fuller and more economic exploitation of the hill resource.

It is of course recognised that practical pastoral systems will be developed in response to considerations other than purely nutritional ones. Economic questions figure largely, and systems which tend to generate their own capital are likely to be more attractive than those requiring substantial initial capital inputs. Labour costs and their likely future trends are bound to have a major impact, and fencing and grazing control offer considerable possibilities in this regard. It seems not unlikely that both technical requirements and economic pressures will operate in concert in determining future patterns of hill pasture management.

5. THE GRAZING ANIMAL IN VEGETATIONAL CONTROL

I. A. NICHOLSON

Summary. This section gives a brief outline of an approach to upland range problems which is based on an examination of some of the factors which are significant in the relationship between grazing animals and their supporting soils and pasture. The general hypothesis is that by the appropriate manipulation of grazing animals, the creative aspects of animal influence can be harnessed to promote a degree of ecological upgrading in hill situations to form the basis of much higher levels of animal output in extensive pastoral systems. Several experiments are referred to in a range of studies extending from small scale critical experiments to a large scale experimental operation.

EXPERIMENTS on the 'reclamation' of upland sites have been carried out intermittently for many years. The concept involves enhancing the soil status to the point where the original semi-natural vegetation can be replaced by a seeded grass-legume sward. In this way production can be increased many times and the increased intensity of use facilitates the application of an array of techniques to promote a high degree of management control. On many farms the lower hill slopes have been enclosed and reclaimed in this way. One effect of this policy is to accentuate the problem of utilising or upgrading the residual hill area whose overall value is reduced disproportionately to the area removed from it. In fact, an analagous problem arises with afforestation.

In hill farming the area which is unsuitable for direct upgrading for economic or logistic reasons is utilised to give the greatest immediate benefit to the grazing animal by the cheapest available methods. The management of the pasture is thus animal-orientated. The consequences of this philosophy and the extent to which it precludes the attainment of future output at higher and sustained levels are rarely considered. It is by the definition of principles of pasture and soil management that we may expect to realise a higher proportion of the potential which is available for animal production in many upland areas.

The detailed examination of contrasts on either side of long-established fence-lines in many parts of Scotland has demonstrated the nature and magnitude of the divergent developments which can occur from common origins. This differentiation in site characteristics has often resulted from apparently slight differences in use over long periods. Most of our hill soils and hence the value of the pastures they support have been modified in this way, usually in an undesirable direction. The principal agent is the grazing animal and the way it is managed. The kind of changes which have taken place are indicative of trends which may be more rapidly induced at higher use intensities.

A fundamental requirement in range systems is to manage the soil and through it the vegetation for the provision of livestock nutrition. In many circumstances the most realistic way of achieving this is by influencing the soil indirectly through the appropriate control of the animal in vegetational use. The harmful effects of grazing, particularly by sheep, are often stressed but there are positive aspects of animal influence which, under management, provide means of asserting the directional control of both soils and pasture so conspicuously absent in upland grazing systems. This concept of exploiting the controlling influence of the product of the system, with a minimum of other inputs, has obvious economic and ecological attractions.

Most soils are able to support alternative types of vegetation to those which are present and in balance with current use and grazing pressure. Studies on contrasting soils, namely on blanket peat on the west coast and on podsolised soil in the eastern Cheviot area, are being conducted to expose the range of different pasture types associated with each when differentiated by contrasting regimes of defoliation. After two years, marked differences in the responses of the two sites are already evident. On the peat site, severe defoliation depresses all species, leaving an exposed unstable surface easily eroded. In its original state, *Calluna* was the most abundant plant of grazing value, and the results suggest that management should be directed towards maintaining the dominance of this species. In contrast, on the *Nardus*-dominated mineral soil site, all defoliation regimes which depress *Nardus* encourage the dominance of other graminaceous species which maintain cover and offer animal diets of higher value. The precise species composition of the induced alternative communities depends on the seasonal application of defoliation. They are also considerably influenced by nitrogen which was applied in one experiment at 100 lb./acre/annum in equal monthly dressings. *Festuca ovina* and *Deschampsia flexuosa* in particular respond to this treatment. Dry matter production between February and October is also markedly increased by nitrogen treatment. This site is thus a good example of a pasture type where the positive aspects of animal influence might be exploited for the benefit of production without deterioration of the site.

In the extensive use of grazing lands, particularly those which for various reasons are heterogenous in their soils and vegetation, there is a two-fold problem. Firstly, the edaphically sensitive and floristically narrow spectrum sites require conservative grazing to maintain the habitat; secondly, on the more stable soils with broader floristic spectra, especially where there is a marked disparity between consumption and growth in the growing season, the need is for the grazing pressure to be increased.

The accumulation of herbage in summer generally results in winter carry-over of dead material, and this inhibits the selection by the animals of high quality plant parts which may still be present. On brown forest soils bearing *Agrostis/Festuca* grassland this problem is less prominent owing to the high preference for this pasture within the hill mosaic. In contrast, on *Nardus* pastures for example, where the dominant is neglected in the growing season when alternative species are available, the problem is more pronounced. In a free-range grazing system there is an inertial factor associated with such pastures, the animals moving elsewhere just at the time when sustained grazing would be most beneficial to the future development of a higher value pasture type.

Experimental studies with sheep on a *Nardus*-dominant pasture have shown that at high stocking rates (14-20 sheep/acre) living *Nardus* is grazed more readily than some other plants, generally regarded as less preferred, particularly if successive 'generations' of new shoots are encouraged by sustained grazing pressure. Unfortunately, an attempt to maintain pressure results in a decline in animal performance. It is interesting to note, however, that in one experiment with cattle this did not occur. There are indications, however, that the performance penalty in sheep declines in successive years. More highly preferred grass species with less strongly developed structural elements tend, under continuing grazing influence, to replace the dominant *Nardus*, e.g., *Anthoxanthum odoratum*, *Agrostis* spp., *Festuca* spp. and *Deschampsia flexuosa*.

The concept of control in extensive pasture use thus involves the acceptance of an energy component as feed-back to the pasture to maintain or enhance its structure, successional status and nutritional value at an optimum in relation to the soil type which supports it. This requires a knowledge of the successional and nutritional potential of component site types in the pasture mosaic, an understanding of animal reactions in terms of movement in relation to the mosaic pattern and changing pasture conditions throughout the seasonal cycle. The integration and control of these factors to satisfy the requirements of animal production without transgressing the needs of conservation or sustained use is the key to successful pastoralism on range-type land.

An *ad hoc* study on typical blanket peat in western Argyll has demonstrated one way in which the conflicting needs of long-term site management and those for immediate animal output may be reconciled. For 10 years, an area of 1000 acres has been used experimentally for this purpose. The principle was to increase the numbers of sheep each year while at the same time adopting a policy of range-orientated measures of pasture management.

Initially the problem was to provide a paddock on the lower slopes which would be the first of a series designed to increase the capacity for grazing control at certain periods of the year. To overcome the animal performance penalty associated with high stocking rates on vegetation previously in balance with a system involving low sheep densities in conjunction with periodic burning, a scheme of limited direct land improvement was adopted. The purpose of this was to increase the spatial heterogeneity of the herbage by providing in mosaic fashion high quality pasture on about 20% of the first 100-acre paddock. Thus the entire flock could be supported for considerable periods on this area. The overspill in grazing from the improved areas eliminated the need for heather burning and encouraged the development of a more desirable growth form of *Calluna* for grazing purposes. This, combined with a centrifugal deposition of dung and urine from the centres of improvement, has brought about a marked upgrading in the grazing value of the entire paddock. A second 100-acre paddock has since been added and treated similarly. By integrating these paddocks with the unimproved hill and by the application of straightforward husbandry practices which the existence of enclosures has made possible, the stocking rate of the area has been increased by 75%, output has been more than doubled and individual ewe performance has been improved.

The present structure with two paddocks and an 800-acre area of residual hill land is now proving inadequate and the need for further control of grazing on the hill proper is evident. The less stable soils with narrow floristic spectra on the peat-capped summits have been exposed to excessive grazing while the vegetation of the intermediate slopes is relatively neglected. There is a clear need to arrange a further fencing pattern to take account of the need to limit grazing at the higher elevations.

This programme, comprising small scale critical studies and heft scale manipulation designed to study the impact of the animal on its pasture, is closely linked with studies on soils and nutritional problems. The grazing animal is regarded as an important determinant of its own habitat and, by understanding the mechanisms involved, there are clearly opportunities for the appropriate integration of use systems within environmental limits at higher levels of animal output without excessive inputs. The emphasis is placed on the evaluation of site potential and capacity for change, rather than on attempts to utilise characteristics of existing vegetation, advantageous to animal production in the short term, in ways which tend to cause destructive changes or alternatively tend to maintain the current sub-optimal conditions.

6. LIFE-TIME PERFORMANCE OF THE BREEDING EWE

R. G. GUNN

Summary. The existing situation is outlined and discussed. In particular, the young growing animal and the nutritional influences which act on it are discussed in relation to its overall life-time production. Current research acknowledges the fact that undue emphasis has in the past been placed upon winter nutrition alone, without due consideration of the effects of improved nutrition at other times of the year. Current results demonstrate the considerable response in terms of fertility which can be achieved with the existing breeds by removing certain nutritional limitations.

IN hill farming, sheep flocks are usually of the self-replenishing type. There are various reasons for this, such as the need for hefting on unfenced hill areas, for resistance to tick-borne diseases, for regular age groups to satisfy subsidy requirements and, not least, for the very nature of the farming enterprises and their geographical locations, with limited capital available for rapid turnover and expensive transportation.

Ewe lambs are therefore retained from each year's lamb crop and either remain with their mothers when all other lambs are weaned or are removed for some form of preferential treatment over a short or long period of time. In the past the greatest emphasis has been placed on the wintering of these ewe hoggs on the assumption that this was the crucial period of the year, with generally severe undernourishment occurring at what was believed to be a relatively important period in the growing animal's life. Certainly the winter period is important but work done by H.F.R.O. suggests that it is much less important than the first and second summers of life to the overall growth and survival to 2 years.

The picture is one of a low level of nutrition throughout the year. Lambing percentages are low. Undernourishment during late pregnancy leads to small lambs and often heavy losses at parturition; a late spring means undernourishment during lactation and hence retarded lamb growth, then, just when grass is beginning to form a significant part of the lamb's diet, the quality declines and lamb growth continues to suffer. The overall result is that the lambs available for retention are both few and small. For example, in the past, some 75% of Scottish Blackface (B.F.) ewe lambs alive at weaning at Lephinmore have had to be kept to maintain numbers, leaving little room for selection and resulting in a poorer standard of hogg than at Sourhope, where only 53% of B.F. ewe lambs need to be kept.

From weaning (August) onwards, the picture is frequently one of little or no live-weight increase, which means that although some growth continues, it is at the expense of body condition previously laid down. The resulting hogg is inadequately equipped to survive a winter characterised by a long period of sub-maintenance nutrition. It is therefore little wonder that the winter treatment of hoggs reared under such poor levels of summer nutrition takes on such importance in the eyes of the farmer. Without raising the level of winter nutrition, many hoggs would not even survive the winter, let alone grow.

Improved Winter Nutrition

Various techniques of preferential wintering are applied in different areas, such as wintering on reseeds, on arable crops, in sheds with hand-feeding, or away from home on low-ground farms. All have disadvantages, mainly in terms of labour and cost. All give very variable results in terms of growth, and the response has been shown to be strongly influenced by the degree of maturity reached during the previous summer. Our work on hogg wintering certainly indicates that animals that are retarded by 6 months of age are beyond the stage of growth and development where improved levels of winter nutrition are likely to overcome this retardation, whereas hoggs well grown by 6 months are able to withstand a substantial degree of winter undernourishment without lasting detriment.

There is now also some evidence to suggest that hill breeds may exhibit a cyclical response in terms of metabolic activity, with a lowered rate during the winter. This may be part of the physiological basis of 'hardiness' but the price to be paid may be a limited response to winter supplementation.

The present conclusion is that nutrition in the first winter becomes less important as nutrition in the first summer is improved; the better the summer nutrition and hence the better the growth during the first 6 months of life, the easier and cheaper can be the wintering.

During early summer in the second year of life, growth response is strongly related to growth the previous summer and to some extent to winter treatment. This is the time of year when nutrition is at its highest level, but unfortunately it falls off during later summer so that by first mating at 18 months the ewes are probably in declining body condition. This is hardly conducive to a high level of lamb production in the following spring. This, in itself, allows the ewes to continue growing and raises the level of body condition, thus enabling the following year's production to be slightly better. This process is repeated over the next 2-3 years with a gradually increasing level of production. For example, at Sourhope, with hill-wintering of hoggs and no supplementary feeding except in storm, live-weight prior to mating increased each year and was associated with an increase in the proportion of twin births and the percentage of lambs marked per ewe alive at lambing (Fig. 1).

There is evidence, however, that increasing the rate of early growth beyond the capability, or what can be termed the 'environmental threshold', of an area, although raising the level of early production, results in only limited increase in later life. The level of adult nutrition is often too low to permit an increase in subsequent production with age. The only gain would therefore be the increased early production. However, there is also evidence that this advantage is lost during the last productive year or two, the more rapidly grown animals actually producing less, as well as being more prone to die, as was the case in experiments at Sourhope with the two Cheviot breeds (H.F.R.O. 3rd Report). A further illustration is the situation at Lephinmore where B.F. hoggs are wintered away and achieve a growth pattern in excess of what they would at home. This enables them to produce first lambs which are 0·45 kg. (1 lb.) heavier than those produced by the B.F. at Sourhope, which are hill-wintered as hoggs. With advancing age, production in the Sourhope sheep improves considerably but in the Lephinmore sheep it shows little improvement except in terms of a reduction in barrenness and lamb mortality.

Different areas obviously have different 'environmental thresholds' and appreciation of this is shown by the farmer's acceptance of the principle of breeding stock bred on the farm (although this might be obscured by the other two main factors, hefting and tick immunity). What has not always been generally appreciated is the relationship between this and life-time production. The evidence suggests that it is in terms of ability to survive that animals reared at levels of nutrition higher than they are going to experience in later life are less efficient.

It is concluded that small nutritional improvements in rearing treatment will result in little productive response over the full life-cycle of the flock unless comparable improvements are made in adult nutrition. This has been done to some extent at Lephinmore by raising the standard of late pregnancy nutrition by hand-feeding, but most of the improvement is probably due to the saving of more lambs through closer supervision associated with hand-feeding and it is

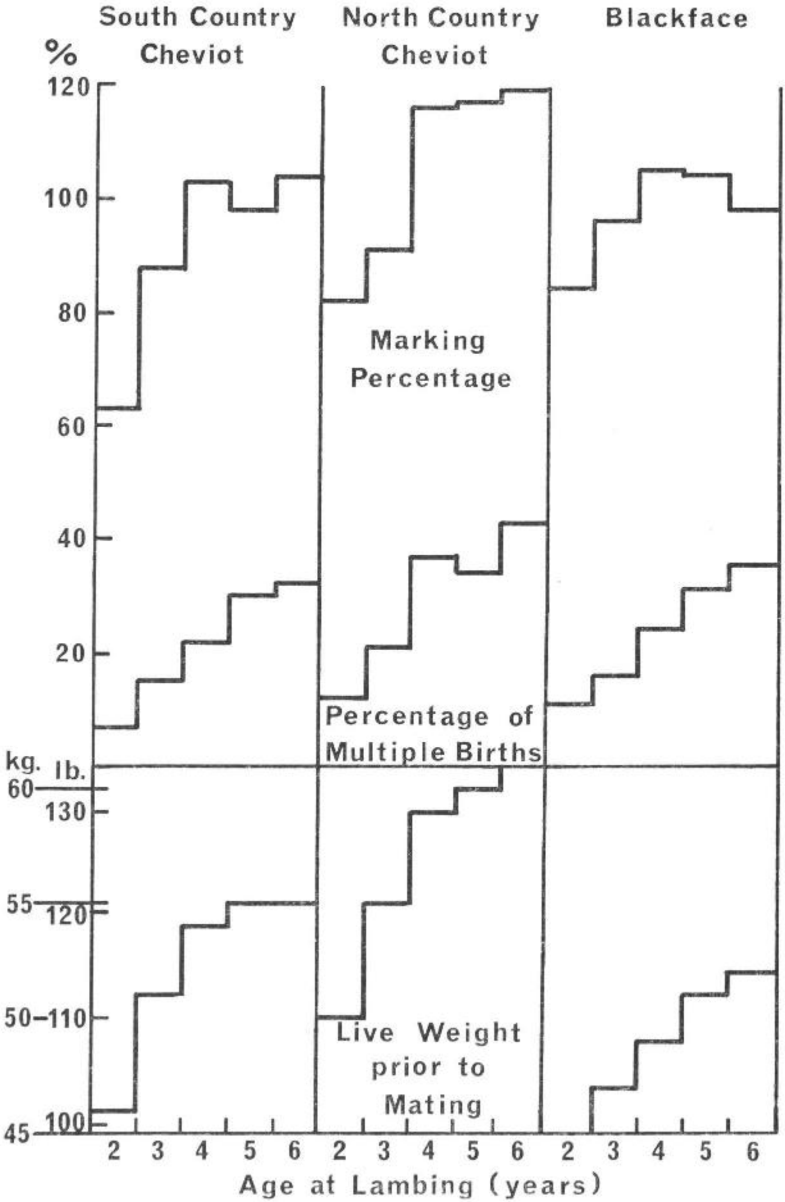

FIG. 1—Changes, with increasing age, of live weight prior to mating, percentage of multiple births, and percentage of lambs marked per ewe alive at lambing (averages over 8 years at Sourhope).

doubtful if the return is sufficient to warrant the extra cost of feeding. However, without hand-feeding in late pregnancy there would be no justification for expensive away-wintering of hoggs and some cheaper alternative would suffice.

Summing up the existing situation, it appears that productive performance in hill sheep is generally low due to a short period of summer growth of herbage, a resulting low level of mid- to late-summer nutrition and hence inadequate and probably declining body condition at mating in November, aggravated by an even poorer level of winter nutrition, and complicated by an environment/rate of growth interaction. Weaknesses in the system are the difficulty of achieving satisfactory body condition during the summer and the low level of lamb production in the younger age groups, the shortage of numbers for quality selection of replacements and the satisfactory rearing of these replacements. All are directly or indirectly due to the relatively low level of nutrition which prevails not only in winter, but throughout the whole year.

To improve production from hill sheep, some, if not all, of these weaknesses must be overcome. Obviously the simple way is to raise the level of nutrition throughout the year and equally obviously this is quite impossible in many situations. There is often neither the ground suitable for improvement nor the capital available to improve it, and in such areas there is probably little future in contemplating any form of substantial improvement in production per animal.

However, production can be improved in those areas where some form of intensification can be practised. By intensification is meant increased production per acre and implicit in this is increased production per ewe, which is the aspect being considered here.

Within the existing systems of management it is possible to visualise several tactical approaches to improvement. These can be, and usually are, aimed at certain obvious and specific weaknesses, but when applied in isolation most are unlikely to give more than marginal improvement. Evidence is accumulating, as discussed previously, that some tactical measures, such as improved winter feeding of hoggs, may give no return at all over a ewe's lifetime. There is evidence, however, that when a series of such measures are integrated they interact to give greater improvement than the sum of the individual measures individually applied. Examples are flushing at mating, late pregnancy feeding, use of improved pasture, etc. The combination of a series of these leads to a new strategic approach. We know that the potential productive capacity of the hill breeds is high, and we consider that the main limitation to the expression of this potential is nutrition. It is therefore of urgent importance to obtain information on the effect of removal of some of the nutrition limitations *in the hill environment*. This information is needed in the first instance to give some idea of what can reasonably be aimed at, as far as the animal is concerned. It is, however, obvious that some clues about how to achieve, or go some way towards achieving, this in practice will also emerge.

Two experiments have been set up to study this. In neither experiment to date has any attention been given to improving winter nutrition (mid-Dec. to late Feb.). More lambs born per ewe can only come from better body condition at mating in the autumn; the ewes would therefore be better equipped to tolerate sub-maintenance levels of nutrition in winter.

Improved Summer Nutrition

In the first experiment, at Glensaugh, improved spring, summer and early autumn nutrition is ensured by giving ewes free access to improved pasture from the hill, initially with 0·25 acres improved pasture per ewe, now reduced to 0·20 acres per ewe. Spring and summer grazing is concentrated on the 11 acres of improved pasture and late autumn and winter grazing on the 40 acres of heather-dominant hill pasture.

In the first year, ewe lambs achieved mean live-weights at 6 months of 42 kg. (93 lb.), lost nearly 20% of this over the winter in declining to 34 kg. (75 lb.) and were mated at 18 months weighing 61 kg. (133 lb.). This resulted in some 61% multiple births and a fertility rate of 145% (lambs born per ewe alive at lambing). Production increased to 65% multiple births and 165% fertility rate in the second year and to 73% multiple births and 175% fertility rate in the third. Future interest centres on the ability of these ewes to continue producing at these levels, but it has been demonstrated that the potential production is high from early in life. Both B.F. and North-Country Cheviot (N.C.C.) ewes are involved in this experiment, mostly single born, and although the N.C.C. have been consistently heavier throughout, there has been little difference between the breeds in fertility.

Improved Autumn and Early Spring Nutrition

The second experiment, at Sourhope, is designed to determine the potential production of all three Scottish hill breeds on hill ground when the main nutritional limitations to production are removed by hand-feeding before and during mating and during late pregnancy and early lactation. Until 1961 the experimental hill area carried South-Country Cheviot (S.C.C.) ewes and hoggs stocked at 0·6/acre and seldom showing a fertility rate of more than 110% with about 20% multiple births, increasing from 7 to 32% with increasing age. From 1961 to 1964 stock numbers were increased to about 0·7/acre without change of management and although overall flock production was practically unchanged the incidence of multiple births in 2-year-old ewes virtually disappeared.

In 1965 the area was stocked with approximately equal numbers of ½, 1½, and 2½-year-olds of each of the three breeds, S.C.C., N.C.C., and B.F., raising the stocking rate to 0·9/acre. Hand-feeding was carried out prior to and during mating of the two older groups for a total of 45 days, during which time approximately 25 kg. (½ cwt.) of a dried grass/maize pellet was eaten/head. Initial inexperience of concentrated feed reduced the effect of this period of supplementation, many animals taking some time to start feeding and some eating very little. Hand-feeding began again 6 weeks before lambing and continued for a total of 77 days, because of very late spring growth of herbage, during which time approximately 50 kg. (1 cwt.) was eaten/head.

Response was limited in terms of multiple births, the incidence being 16%, 18%, and 48% for S.C.C., N.C.C., and B.F. respectively, compared with mean values for the same two age groups over 8 years of 11%, 16%, and 13%, with ranges of 0-20%, 10-24%, and 5-25%. The B.F. value must be considered in the light of the fact that the 3-year-old age group had better nutrition in early life than the rest of the flock, illustrating the rate of growth/environment/production relationship discussed previously. Although the Cheviot breeds did fall within the farm flock range for incidence of multiple births, a comparison with the farm flock marking percentage in this specific year shows that, in terms of ewes mated, 84%, 87%, and 126% respectively, of experimental lambs were marked at a mean 5 weeks of age compared with 77%, 73%, and 84% for the farm flock, which contains the full five age groups of each breed. The presence of three older age groups in the farm flock disguises a much greater differential in what was a severe winter and spring.

In 1966 a new age group of hoggs was retained, the stock now comprising ½, 1½, 2½, and 3½-year-olds, raising the stocking rate to 1·3/acre. In the light of the previous year's results a greater emphasis was placed on introducing the flock to hand-feeding with a view to achieving a satisfactory level of body condition by mating. Feeding therefore started 6 weeks before mating of the three older age groups, which was also advanced by 2 weeks from normal, and continued for a total of 63 days, during which time just over 38 kg. (¾ cwt.) of a dried grass pellet was eaten/head. Hand-feeding began again only 3 weeks before lambing in 1967 and continued for a total of 42 days, during which time less than 38 kg. ($\frac{3}{4}$ cwt.) was eaten/head. At this point, the aim of the experiment must be re-emphasised. It is to determine what the animal is capable of in terms of lamb production when some nutritional limitations are removed. At this stage no attempt is being made to consider the feed inputs on an economic basis.

With substantially improved body condition at mating, response has been considerable in terms of multiple births, the incidence being 40%, 46%, and 70% for S.C.C., N.C.C., and B.F. respectively, compared with mean values for the same three age groups over 8 years of 14%, 23%, and 17%, with ranges of 2-25%, 17-31%, and 7-26%. Fertility rates of 129%, 143%, and 156% were recorded.

Results to date therefore confirm that production in terms of lambs born can be greatly increased merely by ensuring that ewe condition is high and rising at mating. Further interest centres on whether there are any carryover effects of this pattern of improved nutrition into later years. Present evidence from one other experiment (Section 8) suggests that the benefit to the ewe, in terms of improved body condition, of heavy hand-feeding in late pregnancy is lost by the end of lactation, and that extra feed given in early lactation goes into milk production. It must be noted that lambs and hoggs have to date received no special treatment other than additional feeding at the same times as the ewes, and this may obviously be inadequate or unsuitable for the type of growth pattern which will allow fuller expression of adult productive potential under the treatment used.

The potential is undoubtedly high, particularly in the B.F. breed, but it is too early yet to suggest that the Cheviot breeds have a lower response to flushing or a lower fertility/feed ratio. It is in the long term that the greatest challenge lies, in terms of the changes in management and inputs which are necessary to take advantage of these findings in practice.

7. NUTRITION OF THE PREGNANT EWE

A. J. F. RUSSEL

Summary. Free-grazing hill ewes are generally undernourished during late pregnancy. Field investigations have shown that the severity of undernourishment of individual ewes is determined largely by foetal weight.

Estimates of the nutrient requirements of pregnant ewes, and of the effect of undernourishment during late pregnancy on lamb birth-weight, were made in an experiment in which prescribed degrees of undernourishment were maintained by adjusting nutrient intakes in late pregnancy according to levels of certain metabolites in blood plasma.

The high energy requirement during late pregnancy cannot generally be provided by grazing at that time of year; the consequent energy deficit is met by drawing on body reserves. Results of a recent study, in which the pattern of maternal weight loss and the changes in maternal body composition and fat distribution were studied during the pregnancy period, have shown that these reserves are very small at the end of pregnancy.

The results of these and other investigations are discussed in relation to current management systems; a new pattern of supplementary feeding is suggested for late pregnancy in hill flocks.

PREGNANCY, in the hill ewe, constitutes a period of high energy requirement at a time when intake of energy from available herbage is exceptionally low. Although it has been widely recognised that hill ewes are invariably undernourished during late pregnancy (i.e. intake of nutrient fails to meet their requirements for energy) there has been little attempt to characterise or measure the extent to which energy requirements exceed possible intakes in different hill situations or under different management systems.

Considerable research has been devoted to the practical problem of feeding the pregnant ewe, but experiments have generally been conducted without knowledge of the likely nutrient deficit, without a reasonable estimate of nutrient requirements, and without an adequate understanding of the quantitative effects of undernourishment during pregnancy on foetal growth, although birth-weight is commonly used as a criterion to assess the success or failure of the treatment imposed. Failure to appreciate the importance of these factors has on occasion led to incorrect interpretation of experimental results. For example, in the Lephinmore and Glensaugh experiments (Section 9, Tables 1, 2, 3), which were designed primarily to study certain aspects of wool production, it was not possible to demonstrate any effect of level of feeding during late pregnancy on lamb birth-weights. The tentative interpretation of this result was that the partition of nutrients in the pregnant Blackface ewe ensured that foetal requirements were fully satisfied, although it was not clear whether this was an attribute of a munificent ewe or a highly efficient foetus. As shown later in this section, however, an appreciation of the physiological inter-relationships governing maternal and foetal nutrition led to an experiment designed specifically to examine the effects of nutrition during late pregnancy on subsequent production. The unequivocal results of this later work necessitated the reversal of earlier opinions.

In reviewing the information available some years ago on the nutrition of the pregnant ewe Thomson and Aitken (1959) adopted absolute gain or loss of body weight of the ewe as an indirect criterion of plane of nutrition in an attempt to find a common denominator on which to base positive recommendations. However, the difficulty of correlating results of numerous experiments lacking precise nutritional and physiological measurements may be judged from a more recent review of the nutrient requirements of ruminants (Agricultural Research Council, 1965) which lists the requirements of pregnant ewes as 'not available'.

As a preliminary investigation in a series of studies on the nutritional physiology of the pregnant hill ewe, 21 free-grazing Blackface ewes were blood-sampled at weekly intervals from approximately 6 weeks pre-partum to 1 week post-partum. These ewes were run with the remainder of the flock on the hill, where they received supplementary feeding, until approximately 2 weeks before lambing, when they were brought down to sown pasture. Plasma free fatty acid (FFA) concentrations, which measure the rate of fat mobilisation and hence provide an index of the severity of undernourishment, indicated that single-bearing mature ewes under this particular management system were subjected to a relatively moderate degree of undernourishment during late pregnancy (FFA = 750 μeq/l compared with normal levels in adequately nourished ewes of < 500 μeq/l). FFA levels in ewes carrying a single lamb in their first pregnancy (1000 μeq/l) and in twin-bearing mature ewes (1150 μeq/l) indicated that the degree of undernourishment experienced by these individuals was considerably more severe. Changes in plasma FFA concentrations in non-pregnant ewes indicated that more severe undernourishment of the pregnant ewes was prevented by the practice of bringing ewes off the hill grazings on to sown pasture before lambing.

This study served two purposes: firstly, it confirmed what had long been suspected but never actually proved, namely, that hill ewes are at least moderately undernourished during late pregnancy, even in a management system where supplementary feeding is practised, and secondly, it characterised the extent of this undernourishment in different classes of ewes in one particular system in one particular year.

There was also a correlation, at least in mature ewes, between the severity of undernourishment in individual animals during late pregnancy and the weight of lamb or lambs born. A relationship between degree of undernourishment and foetal weight had previously been demonstrated by Reid and Hinks (1962) under closely controlled experimental conditions with restricted feeding of individually penned sheep, and the preliminary investigation described above indicated that a similar relationship also existed under a free grazing system with a supplementary feed input, where it was reasonable to assume that all individuals were eating to maximum voluntary intake (Section 4).

An experiment carried out in collaboration with Eadie and Black, with another breed (South Country Cheviot) in a different locality and under a different management system, provided further evidence of the dependence of degree of undernourishment during late pregnancy on total foetal weight. These ewes were also eating to maximum voluntary intake, and a statistically significant relationship ($r = 0{\cdot}7$) was found between the severity of undernourishment and lamb birth-weight.

It was evident from a comparison of the two investigations that although the differences in degree of undernourishment within a group of pregnant ewes with comparable nutrient intakes are largely determined by foetal weights, the degree to which a group as a whole is undernourished is dependent in the first instance on the level of nutrient intake.

The experience and results obtained in these preliminary investigations provided the means to devise an experiment designed to fill some gaps in current knowledge. The objectives were two-fold. The first was to study the effects of undernourishment during pregnancy on subsequent performance, as measured by lamb birth-weights, lactation (and hence early lamb growth rates) and wool production. The second objective was to establish an estimate of energy requirements during pregnancy.

The essential and most important difference between this experiment and others with similar objectives was in design. In conventional experiments on nutrition during pregnancy it has been customary for two or three groups of ewes to be fed at different levels of nutrient intake, and for all ewes in any group to receive equal amounts of feed, with the objective of establishing uniform nutrition within each group. It is evident, however, from the preliminary investigations described above, that the effect of supplying equal amounts of nutrients to all ewes in any one group is to produce, particularly in undernourished ewes, a range of nutritional states which are dependent on the range of foetal weights within each group. It is possible that in the conventionally designed experiment a ewe in the most poorly fed group and carrying a single lamb could be in a superior nutritional state (i.e. less severely undernourished) to a ewe in a 'high plane' group carrying a large pair of twins. The range of undernourishment within any one group may be greater in terms of nutrients than differences in intake between groups.

It has also been customary in experiments of this type to assess the effect of nutritional treatments by measuring differences between groups in lamb birth-weights. If the reduction in lamb birth-weight caused by undernourishment varies as some function of the severity of undernourishment, a less than optimum plane of nutrition will not affect all birth-weights equally; heavier foetuses will be more severely penalised, affecting the otherwise normal distribution of birth-weights in such a way that it may not be possible to demonstrate a significant effect from standard statistical comparisons of group means.

The ability to measure, in physiological terms, the degree of undernourishment in individual animals made it possible to design an experiment in which uniform nutritional states were maintained in all ewes in any one treatment group, irrespective of foetal weight. Three groups of pregnant ewes were used. Those in the first group were fed throughout the experiment in a manner which ensured that no ewe was undernourished at any stage. All ewes in the second group were maintained in a state of moderate undernourishment, approximately equivalent to that found during late pregnancy in free-grazing hill ewes with average-sized single lambs (plasma FFA = 750 μeq/1), while those in the third group were severely undernourished, and maintained in a nutritional state equivalent to that of twin-bearing hill ewes during late pregnancy (plasma ketones = 8-10 mg. acetone/ 100 ml.). These predetermined levels of undernourishment were maintained within very narrow limits by adjusting the feeding of each ewe once a week according to the concentrations of the appropriate biochemical indices of undernourishment in the blood plasma (Russel *et al.*, 1967*a*).

The results of this experiment not only confirmed that undernourishment during late pregnancy caused a reduction in lamb birth-weight, but also provided an assessment of the reduction caused by measurable degrees of undernourishment (Russel *et al.*, 1967*a*). The moderate undernourishment, which is typical of the average found in single-bearing hill ewes, caused a reduction in birth-weight of 10% compared with that found in the adequately nourished ewes in the first group. It is unlikely that an effect of this order will have sufficient effect on lamb survival or growth rate to justify the input of feed required to prevent it. However, the 25% reduction in birth-weight noted in the more severely undernourished ewes would certainly prejudice the survival of twin lambs born under hill conditions.

The effects of undernourishment during late pregnancy on lactation and on pre- and post-partum wool growth are discussed in Sections 8 and 9.

Within each of the undernourished groups there was a close relationship between the amount of food required to maintain the prescribed nutritional states and the lamb birth-weights. The regressions of feed supplied on lamb birth-weight provided an estimate of additional nutrient requirements in late pregnancy of 100 g. D.O.M./kg. foetus (Russel *et al.*, 1967*b*).

Assuming a maternal maintenance requirement of 8-9 g. D.O.M./kg. it can be calculated that a daily intake of 900 g. D.O.M. in late pregnancy would prevent undernourishment in a 50 kg. ewe with an average-sized single foetus, but would cause a relatively severe degree of undernourishment, with a moderate ketosis (plasma ketone concentration of about 10 mg. acetone/100 ml.), in a similar ewe with twins. The complete relief of this degree of undernourishment would require a further 350 g. D.O.M. intake/day. To produce a similar degree of ketosis in a single-bearing ewe, D.O.M. intake would require to be reduced to 500 g./day.

Energy intakes required to prevent undernourishment during late pregnancy in ewes carrying foetuses of different weights are illustrated in Figure 1. These requirements, calculated from results obtained with penned sheep, are considerably in excess of possible intakes of pregnant ewes on hill grazings where maintenance requirements are likely to be higher. Eadie's studies of the annual cycle of nutrient intake (Section 4) suggest that, for the greater part of pregnancy, D.O.M. intake is of the order of 350-500 g./day, rising to 700-800 g. during the month before parturition.

It is important to emphasise that the high levels of energy requirement referred to above exist only for a relatively short period, as illustrated in Figure 1, and represent levels of intake which are

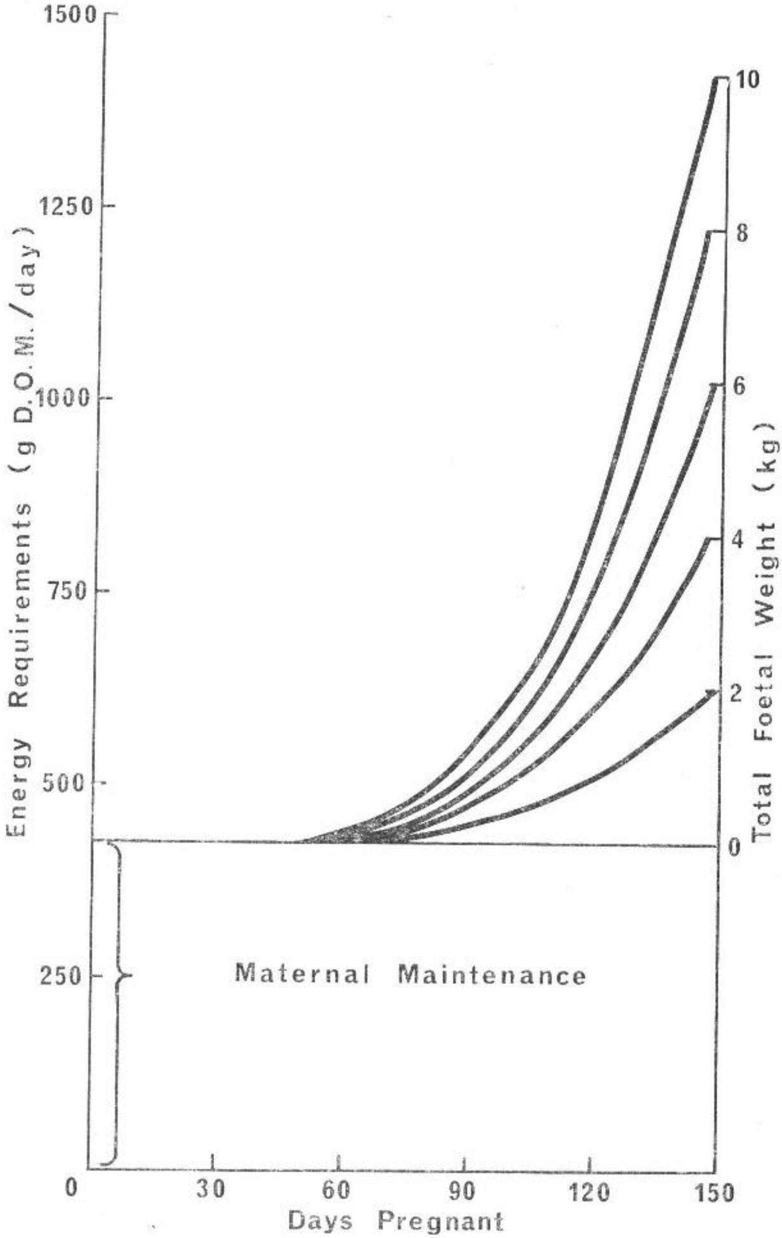

FIG. 1. Theoretical amounts of energy required to prevent undernourisment during pregnancy in 50 kg. ewes carrying different weights of foetus.

necessary to completely prevent undernourishment during late pregnancy. This does not, of course, imply that management systems should be altered in an attempt to completely avoid undernourishment during pregnancy. The sheep is well able to catabolise body reserves laid down at times of plentiful nutrient supply to meet high energy requirements during periods of enforced low nutrient intake.

A recent study of changes in body composition, and particularly of fat distribution, during the complete pregnancy period in a traditionally managed non-experimental hill flock showed that over 20% of the weight of maternal tissue was lost between mating and parturition (Fig. 2), apparently without significantly prejudicing the survival of the ewe. During the first 4 months of pregnancy the decrease in

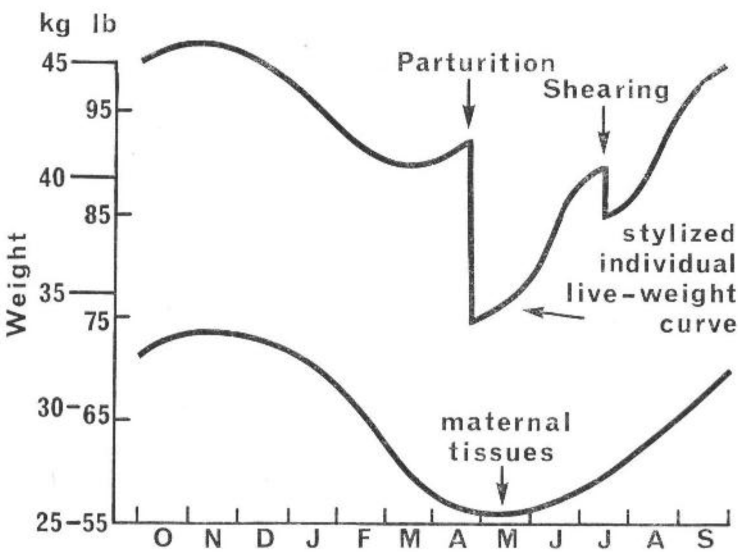

FIG. 2. Changes in live weight and in the weight of maternal tissues of an "average" ewe throughout the year. The difference between the two curves is equivalent to the weights of the fleece, gastrointestinal contents and uterine contents.

weight of maternal tissues (i.e. excluding the weights of gastrointestinal and uterine contents) averaged between 1 and 1·5 kg. per month, and consisted of more than 40% water (principally from muscular tissue) and 30% fat. In the final month of pregnancy, however, 2·2 kg. of maternal tissues containing less than 30% water and more than 70% fat were lost. Over the whole pregnancy period fat reserves were depleted by more than 50%, only 3 kg. remaining in the maternal tissues 1 week before parturition. Examination of the distribution of fat throughout the body at different stages of pregnancy indicated that fat in certain depots is more readily mobilized than that in other sites. For example, during the first 4 months of pregnancy subcutaneous fat reserves were depleted by 67%; a further 19% was lost during the subsequent month. Corresponding losses of fat from skeletal tissue were 1% and 24% respectively. The pattern of fat mobilization noted in this experiment suggests that subjective assessments of body condition (in which subcutaneous fat is the most important single factor) may not provide as good an index of fat reserves as is commonly supposed, particularly at the lower end of the scale. It is noteworthy that incidences of ewe mortality, noted over a period of years, are highest during the months when fat reserves are minimal.

In recent experiments changes in plasma protein-bound iodine (PBI) concentrations, which are used as an index of thyroid function in humans, have been noted in severely undernourished ewes. Two experiments on pregnant ewes have shown that the amount of reduction in plasma PBI concentration during late pregnancy is apparently dependent on the severity of the undernourishment. In a further experiment in which fasted non-pregnant ewes were treated with phloridzin (which causes a loss of glucose in urine and hence a reduction in blood glucose values similar to that found in undernourished pregnant ewes) marked depressions in plasma PBI concentrations were observed. Although the extent to which changes in plasma PBI reflect changes in thyroid activity or metabolic rate in sheep is not yet clear, the lowered concentrations associated with severe undernourishment in pregnant and phloridzinised non-pregnant ewes are tentatively interpreted as indicating a compensatory metabolic adjustment which enables the ewe to withstand prolonged periods of undernourishment.

The ability of the pregnant hill ewe to catabolise body reserves and to adjust metabolic rate may be part of the difficult to define 'hardiness' of hill sheep, and as such can be exploited, at a cost. This cost is measured not only in terms of lamb birth-weight, but, because levels of energy requirement and intake during pregnancy are so inextricably a part of the overall management system, also in terms of conception rate, lambing percentage, lamb mortality, and lamb growth rate.

In management systems dependent on input of supplementary feed during the late pregnancy period, the decision how to make best use of this input is governed by two factors, namely, when and where to apply the input. The shape of the nutrient requirement curves in Figure 1 suggests that a limited amount of feed is better given in progressively increasing amounts over the last 3-4 weeks of pregnancy than at a constant rate over the final 8 weeks, as is frequently the practice. A total input of, e.g., 28 lb. concentrates per ewe is likely to have a greater effect given as, say, $\frac{1}{2}$ lb./day during the 4th week prepartum, $\frac{3}{4}$ lb./day during the third week, $1\frac{1}{4}$ lb./day during the 2nd week, and $1\frac{1}{2}$ lb./day during the final week, than distributed over 8 weeks at $\frac{1}{2}$ lb./day. The latter amount represents a daily input of only 150 g. D.O.M., which is relatively little in relation to later requirements.

It is also inefficient to provide equal inputs of supplementary feed to a group of ewes in which individual animals have widely differing requirements. Any technique which could identify ewes carrying twin lambs, or preferably provide some indication of total foetal weight, would obviously allow more efficient use of the limited supplementary input. A number of workers have reported on the usefulness of radiological techniques in diagnosing pregnancy and determining the number of foetuses, but cost prohibits the use of this technique on a field scale.

The earlier investigations described in this section suggested that estimates of total foetal weight could be made in undernourished ewes with reasonable accuracy from chemical analysis of blood samples collected during late pregnancy. Subsequent experience has proved that this technique can be used very efficiently in closely controlled experimental conditions with animals accustomed to frequent handling and blood-sampling. Under field conditions, however, and with animals which are not accustomed to the procedures involved, the results are less satisfactory, but may nevertheless be useful. Although a certain improvement in efficiency under field conditions could be achieved by minimising the psychological disturbances which particularly affect the plasma FFA and glucose concentrations, this technique can never be 100% efficient, as in any population there is a degree of overlap in the birth-weights of large single lambs and the total weight of twin pairs. Nevertheless the technique merits further consideration and would appear to be suited to conditions of intensive management.

The observations and findings discussed in this section represent results from a continuing programme of research on the nutritional physiology of the pregnant ewe. As the pregnancy period forms part of the complex which makes up the annual cycle of production, so these results, together with other more purely physiological findings which are not relevant in the present context, form part of the better understanding which is required for the development and synthesis of new systems of increased production.

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8. LACTATION AND LAMB GROWTH

J. N. PEART

Summary. Experiments are described which show (*a*) the effect of different levels of nutrition of ewes in late pregnancy on their subsequent milk production and on the growth rates of their lambs, and (*b*) the relative importance of milk and solid food in lamb nutrition, particularly the degree to which an increased intake of solid food can compensate for lower levels of milk intake.

These experiments show that hill lambs have a growth potential much greater than that usually attained in normal hill farming practice. Undernourishment of ewes in late pregnancy need not prevent this potential being reached; a high level of nutrition in early lactation is of far greater importance.

However, for sustained high growth rates, milk production is the critical factor only in the first 6 weeks of the life of the lamb; high growth rates can only be maintained after 6 weeks of age if the quality and quantity of the feed available (e.g., pasture) is high. Any deficiency cannot be adequately compensated by milk.

RECENT and continuing changes in the structure of the British sheep industry, and in the relative importance of sheep products, attaches increasing economic importance to lamb production from hill farms. Though considerable variation occurred between years, mean values taken from the records of the Organisation's farms show that the growth rate of single born lambs reared on hill pasture is 230 g. (0·5 lb.)/day from birth to about 6 weeks of age, declining to 110 g. (0·25 lb.)/day at about 14 weeks. In contrast, intensively reared Blackface lambs have gained 325 g. (0·72 lb.)/day from 0-4 weeks of age and 400 g. (0·88 lb.)/day from 4-12 weeks. These data are illustrated in Figure 1, from which it is apparent that the average daily live-weight gain of the intensively reared lambs was almost double that of comparable hill-reared lambs. Clearly, therefore, lambs produced from our hill flocks have a growth potential which is rarely, if ever, attained in normal practice.

Supplementary feeding of hill ewes in late pregnancy had previously shown responses, if they occurred, in terms of increased number of lambs reared rather than in increased lamb growth (Robinson *et al.*, 1961). Other work suggested that nutrition of the ewe during early lactation was of greater importance to lamb growth (Munro, 1962).

To clarify this point further a feeding trial of hill ewes in late pregnancy and early lactation was made. About 6 weeks before lambing, 63 Blackface ewes were brought from their hill grazing into a field. They were group-fed 900 g. concentrates/head/day, and hay was fed to satisfy appetite. This virtually ensured that all ewes were unequivocally well-fed in late pregnancy (Section 7). As they lambed, the flock was divided into two similar groups of ewes and lambs. One group was put back on hill grazing soon after lambing. The other remained in fields and continued to be fed for a period of 6 weeks after lambing, after which they too were returned to the hill grazing.

The data in Table 1 show that a level of feeding in late pregnancy, substantially better than is given by hill pastures at this time, conferred no advantage in terms of growth rate of single lambs in the first 39 days; the rate of growth was the same as previously recorded for hill lambs (Fig. 1). The data also show clearly the benefit of adequate feeding (as opposed to hill grazing) during the first 6 weeks of lactation. The rate of growth of single lambs was the same as recorded under optimal nutritional conditions (Fig. 1). However,

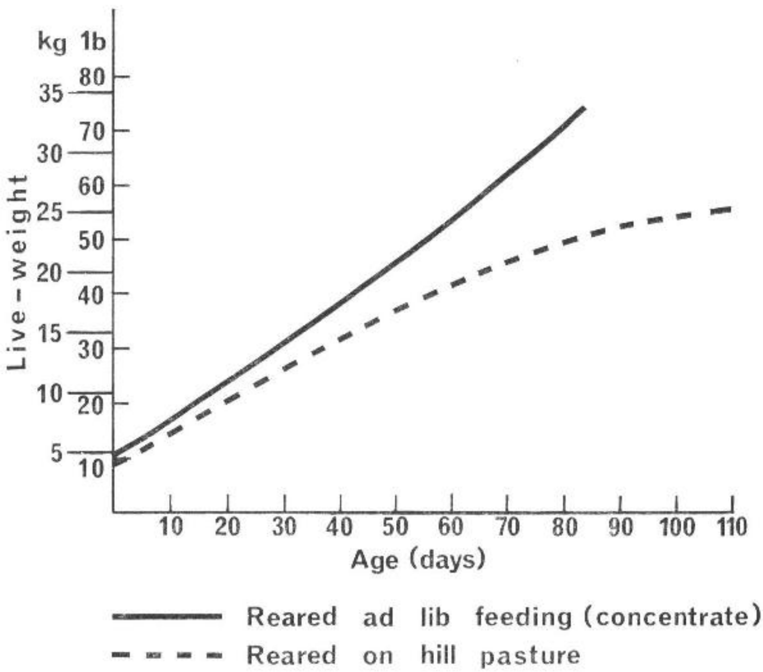

FIG. 1—Growth Rates of Single-suckled Hill Lambs

after the fed group were returned to their hill grazing, lamb growth rates were greatly reduced and the benefits accrued were largely lost in single, but not in twin, lambs by weaning time.

TABLE 1

Mean Live-weights of Lambs (kg.)

	Singles		Twins	
Age	Ewes fed	Ewes not fed	Ewes fed	Ewes not fed
Birth	4·3	4·4	3·5	3·4
39 days	18·2	13·6	15·9	10·5
84 days	25·5	22·7	21·7	18·2
122 days	29·0	28·0	26·7	23·2

The results of this preliminary experiment suggested that a substantial improvement in nutrition in late pregnancy (sufficient to give a live-weight increase of 13 kg. in the last 6 weeks of pregnancy) had no effect on the milk production of ewes with single lambs returned to hill pasture after lambing. From other data it also appeared probable that there was little advantage in terms of the growth-rate of twin lambs.

However, the disadvantage of field experimentation of this sort is that one has to accept the conditions which prevail at the particular time the experiment is done. This may be misleading in a hill environment in which spring pasture conditions, and hence the nutrition of the ewe, vary markedly from year to year.

More precise answers were therefore sought in experiments carried out under controlled nutritional conditions (hand-feeding) in which the level of nutrition of the ewes in late pregnancy could be described in terms of the response of the ewe herself, rather than in terms of feed intake. Data from such experiments can be much more easily related to what happens in the field if the former type of criterion is used.

The first experiment sought to answer three questions:—

1. What is the effect of severe undernourishment in late pregnancy on subsequent lactation when ewes are adequately fed after lambing?

2. Are there important differences between single- and twin-bearing ewes?

3. What is the potential for milk production in Blackface ewes adequately fed in both late pregnancy and lactation, particularly in terms of growth of single- versus twin-reared lambs?

Previous data (Section 7) had indicated the levels of undernutrition likely to be encountered in late pregnancy in free-grazing unsupplemented hill ewes. In this experiment, the food intakes of two groups of ewes were adjusted at intervals during late pregnancy to maintain in terms of plasma free fatty acid and ketone levels, two degrees of undernourishment: a moderate undernourishment (M group) similar to that encountered by hill ewes bearing single lambs (plasma free fatty acid content 600-700 μequiv./1.) and a low level of nutrition (L group) producing undernourishment as severe as that likely to be encountered by hill ewes carrying twins (plasma ketone values 8-10 mg./100 ml.) (Section 7). A third group (H group) were fed at levels sufficient to prevent undernourishment in late pregnancy. A further criterion of the treatment is that moderate undernourishment lowered birth-weights by 10%; severe undernourishment caused a reduction of 25%.

From parturition ewes and lambs of all groups were fed *ad lib.* a pelleted feed containing 66% dried grass meal, 18% maize, 10% soya bean meal and 5% molasses. Milk production was measured at weekly intervals using the lamb suckling technique, from 36 ewes for the first 5 weeks of lactation. Thereafter, the ewes and lambs of group M were discarded and the study continued for a further 5 weeks using 4 ewes with twin lambs and 4 ewes with single lambs from each of the H and L groups. These ewes and lambs were permanently separated into adjacent pens so that individual feed intakes of each animal could be recorded. The lambs were given access to their dams for suckling at frequent intervals each day.

During the first 5 weeks of lactation there was little difference in milk production between groups of ewes with single lambs, and they all reached a similar peak (2·0 kg.) at the 4th week. The ewes with twins from the H and M groups had similar milk yields, but although the L group equalled the peak production (3·0 kg.) at the 3rd week, their production before and after this time was lower than that of the other groups. Throughout the 10 weeks of recording there was little difference in production from the H and L ewes with single lambs. Milk production from all ewes was nearly equal from about the 7th week of lactation onwards. This was regardless of single or twin suckling and, by week 10, production had declined to about 0·65 kg. per ewe.

The average birth-weights of lambs were:— H group: singles 4·8 kg., twins 4·3 kg.; M group: singles 4·2 kg., twins 3·5 kg.; L group: singles 3·5 kg., twins 3·0 kg. Single lambs from the H and L groups weighed 22·0 kg. and 20·9 kg. respectively at 8 weeks of age and 31·0 kg. and 30·6 kg. at 12 weeks of age. Corresponding weights of twin lambs were respectively 20·9 and 17·0 kg. at 8 weeks and 31·2 and 25·6 kg. at 12 weeks of age.

At about 6 weeks of age the average daily intakes of dry matter (solid feed) per kg. body weight of lambs were:—H group: twins 20 g., singles 10 g.; L group: twins 16 g., singles 15 g. Intakes increased rapidly until about 10 weeks of age, then less rapidly during the final 2 weeks. Twin lambs from both groups showed substantially (ca. 15 g. per kg.) greater intakes than single lambs during the period when intakes were increasing rapidly. During the 11th and 12th weeks the average intake of each group of twin lambs was 46 g., and for each group of single lambs 40 g. per kg.

Although the L group ewes with twins did not respond in quite the same way, the data suggest that the feeding treatments during late pregnancy may not have affected their ability to produce milk when adequately fed. It was found in a previous study that about 7 days elapsed before ewes reached peak intake after being on a restricted diet. Therefore, it is possible that the lower milk yield of the L group with twins was partly due to the lower intake of feed early in lactation. Also, the birth-weights of the L group twins were lower than those of the H group and this would reduce the demand for milk. The equality of growth of the H group twin lambs with the single lambs of the other groups despite a much lower intake of milk but with a higher intake of solid feed, demonstrates the potential for growth of twin lambs if given adequate nutrition. The fact that this was not so with the L group twins may have been due to their low birth-weight. The main importance of adequate nutrition during pregnancy may be to produce lambs sufficiently large and vigorous to stimulate milk production in early lactation. These data suggest that, with adequate nutrition, milk production from ewes is a function of the demand for milk by lambs as well as the ewe's potentional to milk. Detailed results of this study have been published (Peart, 1967*a*).

The data in Figure 1 suggest that the inadequacies of hill pasture for lamb growth are expressed in the second half of the growth period to weaning. In other words, it is the quality of the pasture consumed by the lamb which restricts growth, rather than milk production by the ewe in the first 6 weeks of the lamb's life, i.e., before its intake of pasture becomes appreciable. Even so, the previous experiment showed that the intake of solid food by lambs could be increased sufficiently to compensate for the lower intake of milk by twin lambs (i.e., per lamb).

The second experiment therefore sought further information on the relative importance of milk and solid food in lamb nutrition, particularly the degree to which an increased intake of solid food could compensate for lower levels of milk intake. During the mid-pregnancy period, food was rationed to the ewes to maintain a near constant live-weight. This was successfully achieved by feeding 12 g. DM/kg. About 4 weeks before parturition, rationing was discontinued and the ewes were fed *ad lib.* and their individual intakes recorded daily. During the last 4 weeks of pregnancy the mean daily intake of ewes producing single lambs was 40 g. DM/kg. and that of twin-bearing ewes was 36 g. DM/kg. Water intakes increased from 2-3 l./day at 6 weeks pre-partum to 5-6 l./day at parturition.

At lambing, 36 ewes with single lambs were selected for weekly milk recording using the lamb suckling technique. From about 2 weeks of age the lambs were individually offered the same pelleted food as the ewes. The data recorded between mid-pregnancy and 4 weeks post-partum were used to select at the latter time three similar groups, each of nine ewes and nine lambs. Experimental treatments were then applied as follows:—

Group 1. Ewes and lambs continued to be fed *ad lib.* throughout.

Group 2. Ewes fed *ad lib.* throughout. Lambs offered about ⅓ the quantity of solid food being consumed by group 1 lambs.

Group 3. Food intake of ewes restricted to 12 g. DM/kg. based on mid-pregnancy weights. Lambs fed *ad lib.* throughout.

The lambs were separated from their dams and placed in individual pens but allowed access to their dams for suckling at regular intervals each day. Milk recording was continued at weekly intervals until the 10th lactation week. By this time the yields from group 3 ewes had declined to a point when the accuracy of further measurements of milk intake by lambs was doubtful. A final milk recording of groups 1 and 2 was made during the 12th lactation week.

The mean daily milk yield of all groups of ewes reached maximum values of about 2.0 kg. during the 3rd lactation week, declining to around 1·75 kg. in week 4. The mean yields and shapes of lactation curves of groups 1 and 2 ewes were almost identical until the 8th week of lactation. Thereafter, the yield of group 2 ewes was more sustained than that of group 1 ewes, and by week 12 their respective mean yields were 0·85 and 0·60 kg./day.

The effect on milk production of reducing the food intake of group 3 ewes was immediate and dramatic. After 3 days their mean daily yield was reduced to 1·15 kg. and to 0·85 kg. after 7 days. By lactation week 10 the yield had declined to 0·23 kg.

The growth rate of lambs was around 310 g./day during the first 4 weeks. Live-weight data were as shown on following page.

During lactation week 5 the mean intakes of solid food DM by lambs of groups 1 and 2 were 2·8 and 2·1 g. DM/kg. respectively. Thereafter the mean voluntary intake of group 1 lambs rose to 36 g.

Average Live-weights of Lambs (kg.)

Age	Group 1	2	3
Birth	4·8	5·0	4·7
4 weeks	13·2	13·2	13·4
8 weeks	23·0	20·0	21·8
12 weeks	34·2	25·9	31·3

DM/kg. while group 2 lambs were restricted to $\frac{1}{3}$ of this amount. The reduced intake of milk by group 3 lambs was immediately reflected in an increased intake of solid food, from 10 g. DM/kg. during week 5 to 48 g. DM/kg. in week 12, i.e. to a level 33 % above that reached by lambs of group 1.

An examination of the data indicates:—

1. Within limits imposed by single-suckling, ewes of group 1 and 2 were yielding milk to capacity during the first 7 weeks of lactation; group 2 ewes continued to do so until week 12.

2. The small difference in milk production between ewes of groups 1 and 2 was probably due to a reduced intake of milk by group 1 lambs after 7 weeks of age as part of the weaning process. Therefore, any additional suckling stimulus by group 2 lambs did not increase milk production by their dams, but resulted in a more sustained lactation.

3. Whilst group 3 ewes drew upon body reserves for milk production, this process could not sustain yields. This emphasises the dependence of milk production on the level of nutrition during lactation and suggests that with adequate nutrition and in a controlled environment, body condition may have little or no influence on milk yield. Results of current work confirm that any improvement in milk production as a result of drawing upon body reserves is insignificant.

4. Milk production cannot compensate for inadequate solid food available to the lamb, but adequate solid food can go a long way towards compensating for an inadequate milk intake. Full details of this experiment have been published (Peart, 1967*b*).

The main conclusions of work to date can be summarised as follows:

1. Blackface ewes have a high potential for milk production, even when poorly nourished in late pregnancy.

2. This potential is such that the growth rate of twins can equal that of single lambs, a fact hitherto unreported for suckling lambs as opposed to early weaning experimental data.

3. However, this equal growth potential of twin and single lambs is dependent on the twins being well developed at birth and it is in the production of well developed lambs at birth that adequate nutrition in pregnancy is vital.

4. Lactation is the primary factor influencing lamb growth until 6 weeks of age, and this is regardless of the quantity or quality of solid food available to the lamb. Where the quality of solid food available to the lamb is low (as on many hill pastures) the correlation of milk intake with lamb growth may remain high until about 8 weeks of age.

5. Milk production by the ewe depends primarily on her nutrition during lactation.

6. High lamb growth rates after about 6 weeks of age can be maintained only if the quantity and quality of the solid feed available to the lamb is adequate. Any serious nutritional deficiency cannot be adequately compensated for by a higher rate of milk production by the ewe.

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9. NUTRITION AND WOOL GROWTH

J. M. DONEY

Summary. The rate at which wool grows, and therefore annual fleece production, depends on the genetic potentiality of the individual, nutrition, certain non-nutritional influences (such as pregnancy or lactation) and the response to seasonal (probably climatic) factors. Both Scottish Blackface and Cheviot hill breeds grow wool at a relatively high rate in summer (equivalent to that of a wool-producing breed like the Merino) and this rate depends upon their nutrition. During summer, differences amongst sheep are found in both wool growth and in wool growth per unit food intake. In the winter period, particularly during January and February, wool growth is considerably reduced, differences amongst individuals are minimised and the rate of growth cannot be significantly increased by quite large improvements in nutrition. Hence, unlike the Merino, annual fleece weight in hill breeds can only be appreciably affected by nutrition during the 6 months between May and October, and in the first part of this time it is likely to be depressed by the nutrient requirements for lactation.

ONE of the most important factors limiting the fleece weight of grazing sheep is the annual cycle in rate of wool growth. Some degree of periodicity has been found in all sheep but considerable variation exists, dependent on management and breed. At one extreme, fine-wool Merino sheep, maintained on a level annual ration, exhibit a seasonal rhythm with a very small amplitude (Doney, 1966) whilst the feral Soay sheep of St. Kilda have such an exaggerated rhythm that wool growth virtually ceases at some stage during winter (Boyd *et al.*, 1964). The annual rhythm of freely grazing British hill breeds such as the Scottish Blackface and Cheviot is closer to that of wild sheep in that the rate of growth in winter (January to March) can be as low as 10-20% of the maximum rate in summer (Doney and Smith, 1961).

As a protein synthesis, wool growth rate is responsive to changes in nutritional status, although time-lags have been found (Ferguson, 1962; Doney, 1966). Close relationships between the available feed cycle and the wool growth cycle are common in grazing situations (Williams and Schinckel, 1962; Doney and Eadie, 1967). Early work at Lephinmore on grazing Blackface sheep had suggested that the maximum rate was achieved by about August and that a rapid decline occurred after November (Doney and Smith, 1961). The variable influence of pregnancy and lactation on nutritional state made a simple interpretation difficult but it seemed that the wool-growth cycle was consistently out of phase with the presumed feed cycle. A series of experiments was therefore carried out at Lephinmore to clarify some of the questions relating to the interactions of pregnancy, lactation and nutrition in their effect on wool growth rate in the natural environment. The first 2 experiments, described previously (H.F.R.O. 3rd Report), showed that the additional depression of wool growth in pregnant as compared with unmated ewes was very small in winter but considerable during lactation (spring). Furthermore the provision of additional feed between January and March could prevent live-weight loss but had little effect on wool growth. In two subsequent experiments supplementary feed, offered on a group basis to grazing ewes, was regulated in relation to predetermined live-weight curves designed to allow various gains or losses from mating to post-parturition. Certain difficulties in the control and interpretation of group-feeding experiments, particularly during pregnancy, were disclosed (Section 7). Despite this the experiments confirmed previous indications (Tables 1 and 2).

TABLE 1

Blackface ewes. Lephinmore 1963-64. Mean post-partum live-weight expressed as % of weight at mating and mean wool growth in three periods expressed as % of growth rate in July-August

Treatment	Post-partum live-weight	Wool growth		
		Jan./Mid-Feb.	Mid-Feb/ Parturition	Lactation (Mid-April/May)
I Fed to gain 15%	112	21	33	40
II Fed to maintain	98	24	28	35
III Fed to lose 15%	87	24	17	28

TABLE 2

Blackface ewes. Lephinmore 1964-65. Mean post-partum live-weight expressed as % of weight at mating and mean wool growth in three periods expressed as % of growth rate in September-October

Treatment	Post-partum live-weight	Wool growth		
		Jan./Mid-Feb.	Mid-Feb./ Parturition	Lactation (Mid-April/May)
A. Fed to gain 10%	106	40	34	64
B. Fed to lose 10%	80	37	22	56
C. As B to 6 weeks pre-partum. Then as A.	90	35	26	61

In the period between January and February nutritional status had little effect on wool growth but some response was obtained towards the end of pregnancy (mid-April). Wool growth increased during lactation when all sheep were run together on improved pasture. Prepartum feed levels seemed to influence post-partum growth rates in the first year but differences were not significant in the second.

Two experiments involving closer control of nutrition were carried out at Glensaugh during the same period. In the first of these (1963-64) adult Blackface ewes were individually penned after mating (December) and thereafter fed on a pelleted concentrate at rates shown in Table 3. Experience had shown that a rate of 900 g./day of this feed was sufficient to maintain a dry ewe of average weight.

TABLE 3

Blackface ewes. Glensaugh 1963-64. Feed levels (g./day)

Group	Mid-Dec./End Feb.	March	1–10 April
I	1150	1550	1800
II	900	900	1250
III	650	650	1000

Half of the ewes in each group were penned in a sheep-house and the remainder in an outdoor enclosure. Wool growth up to the 9th April (1 week before the beginning of lambing) was not influenced by nutrition or by environment (Table 4).

TABLE 4

Blackface ewes. Glensaugh 1963-64. Wool growth expressed as % of growth rate in July-August

	Grazing Period			Controlled Intake	
Group	15/7–3/9	4/9–7/11	8/11–22/12	23/12–25/2	26/2–9/4
I Sheephouse	100	74	34	21	24
Outdoors	100	70	32	23	23
II Sheephouse	100	71	28	22	26
Outdoors	100	70	37	22	18
III Sheephouse	100	75	37	23	19
Outdoors	100	70	35	24	21

In this experiment and in the group-feeding experiments at Lephinmore mean lamb birth-weight did not differ amongst the nutritional groups.

In a second Glensaugh study a different form of nutritional control was employed. The ration for every sheep was individually adjusted to give one of three pre-determined nutritional states from mid-pregnancy onwards (Section 7). Environment (sheep-house or outdoor pens) had no effect on wool growth and has been ignored in the summary given in Table 5.

TABLE 5

Blackface ewes. Glensaugh 1964-65. Wool growth expressed as % of growth rate in September-October

Group	Grazing Period		Experimental Period		Post-natal period (ad-lib. feeding)	
	27/10–11/12	12/12–28/1	29/1–16/3	17/3–Parturition (22/4 approx.)	P–5/6	5/6–6/7
I Adequately nourished	76	45	18	23	56	105
II Moderately undernourished	78	44	15	10	49	100
III Severely undernourished	80	47	12	6	33	110

In this experiment wool growth in both the immediate pre- and post-partum periods and lamb birth-weight were influenced by nutritional state in late pregnancy. During the first few weeks of lactation there were some differences amongst the groups in amount of feed consumed and in lactation yield (Section 8).

This series of experiments has demonstrated unequivocally that the marked annual rhythm of wool growth in the Blackface hill breed exists independently of any variation in nutrition during part of the year. The consequences of pregnancy and, to some extent, lactation tend to obscure the direct interaction of 'season' and nutrition. Variation in nutrient intake during late pregnancy has produced variable results. There are three possible reasons for which there are no data to allow discrimination. Firstly, the great increase in nutrient requirements due to the rapidly developing foetus may be sufficient to reduce the substrate available for wool growth to a level below that necessary to support the normal seasonal minimum growth rate unless supplementary nutrients are made available to meet this demand. Secondly, physiological changes in late pregnancy may further disturb the endocrine balance which regulates seasonal 'efficiency' of wool growth in the non-pregnant sheep. Thirdly, the timing of the natural wool growth cycle may not be exactly repeatable, and the standard lambing time (April-early May) is in the borderline period between maximum depression (winter) and maximum output (summer and early autumn).

Two experiments were therefore carried out on unmated sheep at Sourhope, using the Cheviot breed which had been found to exhibit a similar annual rhythm to that of the Blackface. Wool growth rate was measured on eight Cheviot wethers at approximately monthly intervals for $2\frac{1}{2}$ years (Doney and Eadie, 1967). These sheep were part of an experiment designed to measure the annual cycle of grazing intake (Section 4). Analysis of periodic regression showed that both nutrient intake (D.O.M.) and wool growth had similar but out-of-phase seasonal cycles. In general, wool growth in July-October was between 10 and 12 g./day (intake 600-1200 g. D.O.M./day) and in January to May fell to between 2 and 4 g./day (intake 300-900 g. D.O.M./day). The relation between intake and wool growth, within and between seasons, suggested that the similarity of the two cycles depended on the correlation of each component with an independent seasonal variable.

In the second experiment at Sourhope an experimental rather than observational approach was adopted. Cheviot sheep in outdoor pens were given the same annual total amount of feed, offered in three ways:—(*a*) at a constant level, (*b*) in simulation of the natural intake cycle and (*c*) with the natural cycle reversed (Doney, 1966). In the group fed within the natural sequence for grazing ewes the wool growth curve was similar to that found in the observations on grazing sheep (maximum growth in July-September approximately $3\frac{1}{2}$ times that in December-February). At a constant feed level the same cycle of wool growth was found (maximum approximately twice minimum) and even when the nutritional cycle was reversed the wool growth rate in summer was 50% greater than in winter. Between December and April wool growth rates did not differ significantly amongst the groups whereas the differences were highly significant between May and October.

The conclusion drawn from these studies is that Scottish Blackface and Cheviot sheep, two very different examples of British hill sheep, exhibit a distinctly seasonal wool growth pattern such that in the winter months the growth rate is depressed and is not responsive to nutritional variation. The annual rhythm may be maintained by internal physiological balance which, in turn, may be related to some independent cyclic, environmental factor such as daylight length, temperature etc. The similarity between intake and wool growth cycles in natural grazing conditions suggests that both may be influenced by similar climatic variables.

Climate has been shown to have a direct effect on wool growth rate. Wind exposure produced a local cooling effect on the exposed side (Section 10). Skin temperature and blood flow rate both decreased but heat loss from the trunk sites increased. The length growth rate of both fine and coarse fibres in a Blackface sheep fell by 10% on the exposed side relative to the lee side of the same animal (Doney and Griffiths, 1967).

Genetic differences in wool growth cycles have been studied, partly within the normal hill breeds but mainly by comparison amongst widely divergent genotypes. In the study of grazing intake and wool growth at Sourhope the differences amongst the eight Cheviot wethers in winter wool growth rate were small and non-significant but, despite little variation in nutrient intake in summer, the differences were then highly significant (Doney and Eadie, 1967). This suggests that phenotypic differences in fleece weight depend on intrinsic differences in conversion efficiency, which in this breed are only expressed during part of the year.

Greater differences were found between breeds. The results from English Romney ewes in the 1964-65 experiment at Lephinmore (see Table 2 for Blackface ewes) are given in Table 6.

TABLE 6

Romney ewes. Lephinmore 1964-65. Mean post-partum live-weight expressed as % of weight at mating and mean wool growth in three periods expressed as % of growth rate in September-October

Treatment Group	Post-partum live-weight	Wool growth		
		Jan.–Mid-Feb.	Mid-Feb.– Parturition	Parturition–May (lactation)
A	111	64	60	76
B	85	47	25	73
C	93	45	33	76

Although wool growth was depressed in winter, the Romney ewes appeared able to respond more readily to variation in nutrient intake, particularly when in excess of maintenance requirements.

Sheep of the Merino type ($\frac{3}{4}$ Fine-wool Merino, $\frac{1}{4}$ Cheviot) were included in the reversed nutritional cycle experiment at Sourhope (Doney, 1966). Unlike the Cheviot ewes, the wool growth curves were similar to the nutritional curves in all three groups, indicating no seasonal interference with the wool growth/nutrition relationship. The effect of interaction between nutritional and non-nutritional seasonal factors, therefore, must depend on the genotype of the animal. The differential results were unlikely to have been caused by direct climatic effects since Merino wool growth rate was depressed to an extent similar to that in the Blackface when unilaterally cooled by exposure to a wind (Doney and Griffiths, 1967). In a controlled nutrition experiment at Glensaugh (1965-66), Merino and Blackface ewes gave differential wool-growth responses to variable nutritional states induced during mid- and late pregnancy.

It is possible to speculate on the nature of genetic differences in the regulation of wool-growth rate in relation to differential metabolic responses to 'climatic' and nutritional variation and in relation to known effects of endocrine balance, but experiments designed to this end have not yet yielded any firm hypothesis for testing. Differential responses to environmental interactions in terms of partition of nutrients in a range of nutritional states, changes in metabolic rates and levels of endogenous endocrine activity are all involved in these speculations.

There are several implications of these studies that may be discussed in relation to the output of wool within hill farming systems. Annual fleece weight depends on the genetic potential of the sheep, on the nutritional cycle provided by the management system, and on the level of productivity in terms of foetal weight and milk output. Cross-breeding, particularly with Merino genotypes, can be expected to produce a greatly increased potential wool growth, and the available evidence indicates that, in many cases, this could be greater than that of either parental breed. However, substitution of a breed with high potential wool production in place of the traditional breeds may not result in a significant increase of wool production within a traditional free-grazing system, characterised by long periods of effective undernourishment. It might even be suggested that, in these conditions, the metabolic patterns which permit wool-producing sheep to maintain their potential rate of synthesis during winter could have detrimental effects on overall biological adaptation.

The question of 'quality' of cross-bred wool is also important. In Russia, for example, it would appear that some of the attempts to produce high-yielding, relatively fine-wool sheep for extensive grazing conditions have been unsuccessful in the first instance, due to introduction of a lack of 'hardiness' with the Merino genotype and 'faults' in the wool quality.

Genetic modification of existing breeds by selection can be considered. Heritability estimates of fleece weight (Doney, 1958; Purser, personal communication) and of the fleece components (Purser and Doney, unpublished) in hill breeds are sufficiently high to allow reasonable response to selection for quantity and quality. Correlated responses to selection for wool would still need to be treated with caution within the context of adaptation to the given environment.

The importance of wool production as a factor affecting the choice of management changes such as are discussed in other sections must be recognised as marginal. Wool can only be regarded as an economic mono-culture in an extensive system with low capital and labour costs. Despite this it can be seen that any modifications of management which can be expected to increase animal output (either per head or per acre) is likely to allow for a potential increase in wool output which can be regarded as a 'bonus'. Genetic differences in potential and seasonal response, and the environmental effect of practices such as early weaning, may then be taken into account in the choice of a suitable breed for maximum exploitation of any given system and indeed in the details of the proposed system itself.

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10. BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES OF SHEEP TO CLIMATIC EXPOSURE

J. G. GRIFFITHS

Summary. Grazing hill sheep are subject to considerable variation in their climatic environment. The effects are likely to be severe during only a short part of the year and even during this period the sheep can select the less stressful conditions from the range provided by the combination of weather and ground factors.

Two aspects of the problem of adaptation to environment have been studied. These are firstly, the behavioural responses to the integrated weather situation in the field and the exposure patterns in the natural environment. Secondly, some observations on variation in both short- and long-term physiological responses to key climatic situations—particularly wind—are presented.

THE period of winter undernutrition in grazing hill sheep, coinciding with the period of pregnancy and early lactation, is characterised by a relatively severe climate in terms of low temperature, high precipitation, low solar radiation, and moderate wind. A combination of adverse climate and a low level of nutrition within a physiologically demanding period may pose a critical winter management problem.

The optimum climatic environment of the sheep has never been completely determined. In order to assess the balance between heat production and heat loss within the range of physiological and nutritional variations that exist, it is necessary to obtain specific information on the climatic environment of the grazing animal, on its possible thermoregulatory adjustments within such an environment and on the part played by such factors as adaptation, acclimatisation, fleece insulation and the energy cost of gathering the feed.

The contributions from the Hannah Dairy Research Institute, such as described by Blaxter (1962), clarify the possible energy cost of the environment. However, the static situation in the laboratory cannot adequately represent the field situation. There are three important additional factors: the weather component of climate, the micro-climate variations available to the grazing animal and the behavioural responses of the animal to adverse weather.

The Field Situation

A climatic description of an area is a mean value. Weather components and areal differences are confounded, and consequently such data are of limited value in assessing the relative exposure of the animal. Inability to integrate the various weather factors into a single quantifiable parameter and to assess the direct and carry-over effect of this on the animal is a gap in our knowledge which makes it difficult to calculate the overall climate cost.

Micro-climate variations will fall around the climatic mean of the general area, but their combination will be peculiar to the area studied. There are certain established factors: a general decrease in temperature with height of 1° C in every 300 feet, on increase in rainfall, humidity and wind exposure with altitude and a greater radiation input on south facing slopes. Such information is, however, only relevant to a conical-shaped hill devoid of vegetation. Hill areas are not uniform morphological features, but show a range of shape and geometry and are covered with vegetation of extremely varying form. Such characteristics of the topography extend the range of microclimates within a specific area.

The climatic factor which is most significantly modified by topographic variation is wind. Exposure to wind is dependent on the general and local topography of the area, and the differences in exposure are apparent to anyone spending any time in such areas. To the sheep these differences are even more significant as vegetation has a considerable effect on air-movement patterns nearer to the ground.

Wind has a major effect on the heat loss pattern of the animal; the breakdown of external insulation (i.e. the joint insulation of the air interface and fleece) increases convective heat losses considerably. Figures given by Joyce and Blaxter (1964) show that heat production is increased considerably in wind; for example, a sheep with a short fleece kept at −3° C and in a wind of 4·2 m.p.h. had its heat production increased by 3·3 times that recorded under thermoneutral conditions.

To assess the relationship between the climate of an area and that of the grazing animal is a complex problem. One approach is to examine behavioural responses to specific weather situations, but this requires a detailed background of the 'normal' behaviour pattern, and measurement of the micro-climate of the area where the animal is grazing.

At Sourhope we have attempted to relate the grazing location of a single flock to variations in wind speed over the area. Other weather components have been measured at one site only, since their range of variation is relatively less. Two previous studies (Munro, 1962; Griffiths, 1966) had suggested that at wind speeds above 24 and 22 m.p.h. respectively, sheep moved into shelter and continued to graze.

The distribution of freely-grazing hill sheep is subject to social and territorial associations (Hunter and Milner, 1963). On the area studied there was a pattern of social groupings associated with specific areas of the hill. There was a difference in mean live weight between the two main social groups at the hogget stage but not in later life. Removal of two-thirds of the original flock and their replacement by a 'bought-in' flock created a slightly modified territorial grouping; the new animals appeared to form a loose association with the remnant of one of the social groups, but their grazing tended to be concentrated on the poorer pastures of the territory.

An important factor in grazing behaviour studies is the location of pastures which are preferred by the animal. As expected (Hunter, 1962), the sheep showed a distinct preference for *Agrostis-Festuca* pastures, rather than for the nutritively poorer *Molinia-Nardus* swards. Thus social behaviour and pasture preference determine the main pattern of sheep distribution in any grazing location. Climate and exposure have a secondary effect on distribution and their influence will depend on the climatic exposure of the better grazing areas. Thus when otherwise preferred areas of good grazing were exposed to strong winds the sheep were found to have moved away. If the exposed areas on a hill form the major part of the better grazing areas, the productivity of such areas might be limited because of exposure, with the consequent result of better utilisation of sheltered, but poorer, grazing areas.

These observations focus some of the questions associated with the provision and siting of artificial shelters. Behavioural aspects suggest a preference for shelter above certain critical exposure levels, but the necessity for providing shelter at all times must be questionable. Shelter may only be necessary during the late winter period, when energy demands are at their peak and must then be associated with availability of suitable grazing. Some shelter for the ewe may be essential at lambing and at this time the requirements of the newborn lamb must also be considered.

Lamb losses due directly to inclement weather are difficult to establish, partly because nutrition is a confounding factor, and our attempts to establish an association between lamb mortality and adverse weather within 24 hours after birth have shown negative results. Other factors are involved, and appear to be related to lamb birth-weight. Heat production is increased in the newborn lamb after feeding, and the time-lag between birth and first suckling may be critical in adverse weather. The time taken for this activity was found to be negatively correlated with lamb birth-weight ($r = -0{\cdot}48$). Measurements of rectal temperature at birth, and at 1 and 24 hr. after birth, show correlations with birth-weight of $r = 0{\cdot}46$, $0{\cdot}48$ and $0{\cdot}24$

respectively. This evidence is in line with observations of other workers (Alexander and McCance, 1958) and suggests that at birth and soon after the heavier lamb, with its relatively smaller surface area, loses heat at lower rate than the smaller lamb. At 24 hr. the lamb has developed thermoregulatory controls over heat loss. Thus the smaller, undernourished lamb is at greater risk during the longer interval between birth and first suckling. The availability of shelter for small lambs (e.g. twins) at birth is, therefore, desirable, particularly in hill situations in which twin lambs are certainly undernourished prior to birth.

Fleece Insulation—Effect of Wind

In discussing energy demands of the environment, and possibilities of amelioration through better nutrition, shelter or housing, the physiological responses of the animal and the role of fleece insulation must be taken into account. The only way we can assess these factors is through critical study in controlled conditions. Air movement, generated in a wind tunnel, has been used to study these factors.

Fleece insulation is a physical factor, and in still air is related to depth and density of fleece (Doney, 1963; Blaxter *et al.*, 1966). To date we have measured the fleece insulation provided by Blackface (Lewis strain) and Merino ($\frac{3}{4}$ Merino, $\frac{1}{4}$ Cheviot) fleeces. In still air the shorter but more dense fleece of the Merino seems to provide greater insulation than the longer but more open fleece of the Blackface (56 to 27 °C/k.cals./m.^{2}/24 hr.). In a wind of 13 m.p.h. the insulation of the Blackface fleece was reduced to about 5 units as opposed to 11 units for the Merino fleece. Shearing the fleece to a depth of 3-7 mm. reduced the insulation in still air to a value of 5 units in both breeds.

In homeothermy, where the essential feature is to maintain a balance between heat loss and heat production, we recognise two types of physiological response. Within the thermoneutral range the animal can adjust its heat losses without raising heat production (by changes in body temperature, and by reduction of the temperature gradient between the skin and core). Under more adverse conditions heat production has to be increased to counter the higher rate of heat loss.

In still air, within an ambient temperature range of 5-20° C, the skin temperature of the trunk falls at a rate of approximately 0·2° per 1° C fall in ambient temperature. The temperatures of the extremities remain high with occasional fluctuations. Rectal temperature falls very slightly with increasing ambient temperature. On exposure to strong wind (13 m.p.h.) the pattern changes. Temperatures of the extremities fall either to ambient, or 1 to 2° C above. Skin temperature on the exposed side of the trunk falls by a few degrees to a level related to the ambient temperature; in this situation, where fleece insulation is almost destroyed, changes in ambient temperature are paralleled by similar changes in skin temperature. Rectal temperature may increase for a short period, then falls to reach an equilibrium level.

In observations carried out during winter and spring months at ambient temperatures between −2° C and 9° C some differences in the relationship amongst ambient, skin and rectal temperatures and local rates of heat flow have been observed. These differences may indicate a seasonal pattern in cooling resistance similar to those which have been observed in a number of other species (e.g. Hart, 1962).

Acclimatisation

Exposure to climatic stress in the field can vary considerably in duration, and this situation has been simulated by varying exposure time for periods of up to 6 hrs per day over 2 to 9 consecutive days. During the first day of exposure there was little change in skin, rectal or extremity temperatures after the first hour. On the second day of exposure, skin temperatures were elevated before, and during, exposure. This elevation usually disappeared by the third day. In two full-fleeced animals no further changes in skin temperature occurred during a subsequent week of exposure, but in others a further decline in skin temperature occurred within this period. These changes could not be explained in terms of variation in ambient temperature.

In several other species, and notably in man, there have been a number of attempts to investigate the possibility of acclimatisation to environment (Davis, 1962) and the traditional 'hardiness' of the hill breeds may be linked to this factor. It is possible (Davis, 1962) that constant exposure to adverse weather could result in a conditioning of the organism to such an extent that the effects of climatic stress are minimised. This ability to acclimatise may be affected by housing and some evidence in support of this has come from a study of the rectal temperature response on exposure to wind. The normal pattern of rectal temperature change during severe exposure is a rapid increase, followed by a slight fall to an equilibrium level. Such a pattern is related to a metabolic overshoot as the system adjusts to a different heat loss situation (Webster, 1966). This rectal temperature response was found in all experimental exposures, but the time taken to attain the initial peak was significantly less in sheep kept outdoors. These animals seemed to be able to respond to the cold stress more quickly than animals conditioned to an indoor environment.

The results and suggestions in this section represent preliminary observations on various aspects of a complex problem on environmental physiology in its widest sense, the interaction between animals and their own environment. It is already apparent that much more information needs to be obtained before questions relating to the requirements for natural or artificial shelter and housing can be integrated with those of management systems as a whole. It is evident that the answers will depend to a considerable extent on the nutritional cycle. It can be argued that certain physiological responses to long term climatic stress may have survival value in well-nourished non-pregnant animals, with opportunity to adjust their feed intake. These responses could well be disadvantageous to poorly-nourished animals on restricted intakes having high metabolic requirements imposed by pregnancy and lactation.

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11. TICK-BORNE FEVER AND TICK PYAEMIA

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Summary. It is axiomatic that the maximum productivity which can be derived from any system of sheep management, whether traditional or improved, can only be obtained if losses due to disease are minimised. The occurrence of the sheep tick (*Ixodes ricinus*) and hence of tick-borne diseases in many hill areas thus presents a problem which is of considerable economic importance and for which there is, at present, no satisfactory solution. Present control methods are based on the prevention of tick infestation. Practical difficulties are associated with these methods but paucity of precise knowledge of the aetiology of both tick-borne fever and tick pyaemia limits alternative approaches to control methods. Investigations have consisted of both field and laboratory studies. Field surveys have given precise information on variation in the incidence of tick pyaemia with age and year. Detailed field studies on lambs in the first month of life have been concerned with the incidence of tick-borne fever and the time relationship between its onset and that of tick pyaemia. Some experiments have been carried out on control of these diseases, based either on a reduction in tick infestation or the prophylactic use of antibiotics. Laboratory studies include the response to Staphylococcal infection following tick-borne fever, with particular reference to failure of the inflammatory response, chronic abscess formation and failure of neutrophil migration.

A bioclimate suitable for the survival of the sheep tick (*Ixodes ricinus*) occurs in many hill regions of northern England, Scotland and Wales. Tick-borne diseases thus present a specific problem in these areas, and productivity, expressed in terms of lamb survival and growth rate, is often considerably reduced. Of the three principal diseases, namely, louping ill, tick-borne fever and Staphylococcal infection (tick pyaemia), a vaccine has been produced only against louping ill and is utilised to immunise susceptible adult sheep. There is at present no satisfactory method of preventing either tick-borne fever or pyaemia in lambs. Control methods based on the prevention of tick infestation by dipping or smearing lambs with anti-tick cream at birth have been advocated, but there is a divergence of opinion concerning the efficacy of these methods and considerable practical difficulty when lambing occurs on the hill.

However, the formulation of alternative control measures is handicapped by the lack of precise knowledge of the aetiology and interrelationship of both of these diseases and the present investigations were undertaken to provide further information on this subject.

In order to define the problems more precisely an annual field survey of pyaemia was initiated in 1965 on one particular tick-infested farm in Selkirkshire. All lambs born on one hirsel have been ear-numbered at birth and their subsequent disease history recorded. The data obtained to date have confirmed that pyaemia occurs in lambs between 2 and 7 weeks of age and is rather more prevalent in male lambs than in female lambs. Moreover, the live-weight gain of many lambs which subsequently develop pyaemia is comparable with that of normal lambs, and it does not therefore seem that the nutritional status of the lamb is a primary factor in the aetiology of the disease. The survey has also demonstrated that in a given locality with a moderate to heavy tick infestation the annual incidence of pyaemia may vary considerably, and the results suggest that in years of high incidence the disease occurs in lambs at an earlier age. The cause of this annual variation is of interest since it would be advantageous both experimentally and practically if the incidence of pyaemia could be predicted.

A number of factors may influence the annual incidence, but a similar variation in the incidence of pyaemia has also been recorded in more detailed experiments, discussed later, where it is known that the incidence of tick-borne fever remained constant. Fluctuations in the annual incidence of tick-borne fever may therefore be discounted, and it now seems possible that the varying incidence of pyaemia in different years is related to the immune status of the lambs.

More detailed studies have been carried out, on the interrelationship of tick-borne fever and secondary bacterial infection (pyaemia), on lambs born in an enclosed tick-infested pasture in Roxburghshire. Daily temperatures and blood films from a total of 65 lambs have established that, with one exception, all lambs contracted tick-borne fever within 14 days of birth, the majority showing evidence of infection between the 7th and 9th day. Tick counts have also shown that a very light infestation is sufficient to transmit this disease. Daily weight gain data have confirmed the opinion of McEwan (1947) that tick-borne fever alone is a benign disease in lambs. The only noticeable adverse affect of uncomplicated tick-borne fever has been a slight reduction in live-weight gain for 1 to 3 days during the febrile period, but even this mild and transient set-back was an inconstant feature. In contrast, a very marked reduction in weight gain or even in live-weight was associated with the onset of secondary bacterial infection. A number of authors have referred to the check experienced by young lambs on tick-infested pasture, and it now seems reasonable to attribute this largely to the effect of both clinical and sub-clinical Staphylococcal infection. This agrees with the opinion advanced by Watson (1966), who demonstrated a more rapid growth of lambs on tick-infested pasture following a double dipping routine.

Although the incidence of tick-borne fever remained constant in the 2 study years, the incidence of pyaemia varied. A 12% incidence of the latter disease was recorded in 1965, compared with a 25% incidence in 1966. However, of a total of 13 infected lambs only eight exhibited the joint form of pyaemia. The remainder showed a high erythrocyte sedimentation rate, a marked loss of weight and, on post mortem, abscess formation was present in a number of internal organs. In this latter group of lambs it is clearly impossible to determine when the bacterial infection became established. A more accurate assessment is, however, possible in the lambs with the joint form of pyaemia since the onset of arthritis indicates the presence of the pathogen which may also be confirmed bacteriologically. A study of the time interval between the onset of tick-borne fever and visible arthritic signs has suggested that there is a sequential relationship between these two diseases, the secondary infection becoming apparent in all cases within 10 days of the onset of tick-borne fever. This tends to support the contention advanced by Foggie (1962) that tick-borne fever is one of the factors predisposing to pyaemia.

Foggie has also demonstrated experimentally that during the neutropenic phase of tick-borne fever which succeeds the febrile reaction, the resistance of lambs to Staphylococcal infection is considerably reduced. In the present investigation differential neutrophil counts were carried out for 15 days following the onset of tick-borne fever to provide a guide to the onset of the neutropenic phase and to determine whether secondary infection became apparent towards the end of this period. However, no close correlation has been established and the results suggest that the neutropenia is not necessarily the sole factor involved in reduced resistance to naturally occurring Staphylococcal infection. Under field conditions it seems possible that Staphylococci may become established in at least a proportion of lambs before the neutrophil cell numbers have markedly declined and, although the neutropenia will modify the inflammatory response, other features which may be associated with the earlier febrile period may contribute to a lowering of resistance.

This hypothesis has been studied experimentally and preliminary results indicate a number of possibilities which are currently being investigated. The retention of intravenously injected India ink by the reticulo-endothelial cells of the liver and spleen is considerably reduced during the febrile phase of tick-borne fever. This may indicate a temporary derangement of reticulo-endothelial function which may be causally related to the widespread dissemination of Staphylococci which occurs in many cases of pyaemia. There is also some evidence that inhibition of granulocyte mobilisation may occur in some cases of tick-borne fever several days before the onset of neutropenia, and that experimental Staphylococcal infection at this time fails to produce a normal inflammatory response. The abscesses which develop in such cases become chronic and resemble those frequently found in field cases of pyaemia. It has also been found that an apparent failure of the inflammatory response may occur at the time when the neutrophil numbers are normal, but when a high percentage of the circulating neutrophils contain the infectious agent of tick-borne fever. This observation has suggested that diapedesis of infected neutrophils is inhibited, and initial comparisons of the percentage of infected neutrophils in the circulating blood and in induced peritoneal neutrophil exudates tend to support this theory.

A transient but marked thrombocytopenia of several days' duration which develops approximately coincident with the onset of the febrile phase has also been demonstrated. The diminution in the number of thrombocytes is frequently associated with defective clot retraction but the pathological significance of this observation does not appear to be profound, since only one case of an haemorrhagic syndrome associated with tick-borne fever infection has been recorded.

Until a reliable and convenient means of counteracting these diseases is evolved prevention must be based on standard methods. The use of dips to prevent tick infestation has already been noted and Watson (1966) has shown that a double dipping routine reduces pyaemia. It has, however, been observed that dipping reduces but does not entirely eliminate tick infestation, and since only a small number of ticks are required to transmit tick-borne fever it is difficult to understand why dipping effectively reduces pyaemia. To provide some information on this subject a small dip trial with twin lambs has been carried out. Dipping had a noticeable effect on tick infestation, the undipped lambs becoming more heavily infested. Nevertheless, the dipped lambs acquired a small number of ticks which attached almost exclusively on the lips and the hairless regions of the axilla and groin where the persistence of the dip would be of shorter duration. However, when attachment did occur in the dipped lambs the majority of these ticks died before engorgement.

Tick-borne fever was diagnosed in all control lambs and in one dipped lamb approximately 1 week after exposure to ticks, and all lambs had acquired the infection by the 20th day. Thus, although tick infestation was reduced, dipping did not prevent tick-borne fever. It was, however, apparent that the length of the febrile period in the two groups differed considerably, being shorter in the dipped lambs. The value of dipping may, therefore, lie not in the prevention of tick-borne fever but in a suppression of the severity of the initial attack.

If tick-borne fever cannot at present be prevented attempts may be made to control Staphylococcal infection in endemic areas by the prophylactic use of antibiotic. The relatively wide age incidence of pyaemia presents a problem since there is no antibiotic preparation which will maintain therapeutic blood levels for this period of time. However, since the majority of pyaemia cases occur between 2 and 4 weeks of age the time limits can be reduced. Field trials have, therefore, been carried out with Penidural L.A., a long acting preparation of benzathine penicillin which will maintain a therapeutic blood level in man for 14 days following an injection of 1·2 million units. Lambs have been injected either at birth or in mid-May with this preparation and the incidence of pyaemia and death recorded in these lambs and in an equivalent number of control lambs. The injection at birth reduced the incidence of pyaemia but was not so effective as the injection given in mid-May. The time of injection does, however, appear to be critical and it has now become standard procedure to inject the lambs when the first cases of pyaemia become apparent. The principal disadvantage of this method lies in the extra gathering required for injection, but it does provide a reasonable control in localised areas where the disease is economically important.

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SUMMARY

HILL pastures are the resultant of uncontrolled grazing, largely by sheep, on a vegetation of which the species composition is otherwise dictated largely by low soil fertility and climate. The interaction between grazing pressure, seasonal growth curves and chemical composition of individual plant species leads to a yearly animal nutritional cycle which is sufficient only to support individual levels of animal production which are far below the potential of the existing breeds. This level of nutrition is so low that the body reserves necessary to support the animal during the long period of undernourishment in winter are barely sufficient for the task.

The fact that the ewe is drawing on body reserves over the December-end of February period is probably not, in itself, of any significance as far as production per ewe is concerned. It is the fact that reserves are so depleted by the time that the extra nutritional requirements of late pregnancy and lactation have to be met which has the major effect on production, and this holds whether the ewe has a single or twin lambs. The mortality rate among ewes is highest in the last month of pregnancy and the first month of lactation (Gunn, R. G. (1967). *Anim. Prod.* 9, 263), and this emphasises the importance of adequate nutrition in both these periods, not only in late pregnancy. It must be emphasised that an increase in the number of twin lambs is not the only way to increase the efficiency of production. In fact there is little point in attempting this until substantial improvement in nutrition in late pregnancy and particularly lactation have been ensured. Even with single lambs, a high death-rate in ewes, heavy lamb losses at parturition and slow growth-rates of lambs after 8 weeks of age represent a substantial loss in production efficiency. Under these conditions, which prevail particularly where lambing percentages are, say, 80% or less but, in respect of slow growth rate of lambs, on all hill pastures, it is pointless to make increased twinning rates a priority objective.

Improved efficiency of production on hill farms will come only from substantial improvement in nutrition in spring (late pregnancy and early lactation), summer (lamb growth in terms of pasture, rather than lactation) and autumn (improved nutrition at tupping). Nutrition in the December-February period will actually become less important as nutrition at other times is improved, because improved late summer and autumn nutrition (that is, after weaning) will mean a

higher level of bodily condition and hence of body reserves at the beginning of winter. In any case, improved nutrition in autumn will delay the onset of winter weight loss.

The dramatic response in prolificacy of the existing hill breeds, both to improved nutrition before and during tupping and to improved bodily condition at tupping, regardless of a declining level of nutrition at this time, suggests that substantial increases in twinning percentage will be a natural consequence of nutritional improvement at other times, whether the individual farmer regards this as a desirable objective or not.

Finally, the greater the body reserves at the beginning of winter, and the later these reserves begin to be drawn upon, the longer can provision of extra feed in late pregnancy be delayed, even when the proportion of twins is high. The point is important, because the manner in which soil temperatures in hill areas fluctuate in the February-April period about the critical value for initiation of plant growth, and particularly the year-to-year variation in spring pasture growth which results, makes it likely that adequate nutrition in late pregnancy may only be assured in most years by hand-feeding.

We can see no good scientific reason why any approach towards total amelioration of the effects of the normal winter climate in December, January and February should find a place, for reasons of increased animal production, on most hill farms as long as the existing sheep breeds continue to be used. There will be exceptions but the reasons will usually be obvious and need no discussion here. There are cogent human reasons, and these may eventually become of major importance, but much could be achieved in this direction by relatively simple changes in management, particularly those which are aimed primarily at a degree of control of grazing.

All the evidence in this and previous reports indicates that changes in husbandry techniques alone, without substantial improvement in nutrition over the summer and autumn period, have had, and will have only marginal effects on production from existing breeds. Subtantial improvements in nutrition can be effected in only two ways: (*a*) replacement of existing pastures with sown, exotic species ('reclamation' or re-seeding), and (*b*) radical changes in management of existing pastures by control of grazing.

Re-seeding is impossible over large areas of hill land because of topography or, if possible, is very costly. Most importantly, the areas characterised by soils such as the brown-earths, which are most easily re-seeded, now carry pastures of the *Agrostis-Festuca* type which respond dramatically to grazing management alone. The work done to date indicates that, before any fertiliser inputs are considered, the nutritive value of these pastures can be substantially improved by a greater intensity of grazing.

If such pastures are to be utilised intensively during spring, summer and autumn, with no carryover of senescent material to dilute the quality of the feed ingested in spring, the first problem is that of removal of accumulated dead herbage with a minimum nutritional penalty, particularly if this has to be done with breeding ewes. Several possibilities require investigation. Preliminary work suggests that cattle may suffer a smaller nutritional penalty than sheep. The use of wethers must obviously be considered. Appropriate fertiliser treatment, by stimulating spring pasture growth, would reduce the deleterious nutritional effect of that part of the dead winter herbage of lowest nutritional value, with a digestibility as low as 35%. Mechanical removal of dead herbage offers further possibilities in some areas.

The first research priority, however, is to examine the nutritive value and utilisation of such 'improved' pastures in relation to the various elements of animal production. In theory, the management procedure necessary to provide pastures which will in turn provide the level of nutrition needed to increase the conception rate in the ewe will also provide the higher levels of nutrition needed earlier in the grazing season for the satisfactory rearing of an increased number of twin lambs. In practice the latter may be more difficult to achieve than the former; a relatively small improvement in autumn nutrition as a result of intensive grazing in spring and summer may give a 20% increase in the number of twin births but the improvement in nutrition in spring might be inadequate for the ewe with twins. Likewise there is a very big gap between the level of summer nutrition which results in the present store lamb in August and that which would be necessary to fatten these lambs satisfactorily over the same period.

It is obvious therefore that the effects of controlled grazing alone may not be enough. The problems of encouragement of white clover establishment in heavily-grazed *Agrostis-Festuca* pastures will have to be examined. In some respects at least, conditions at the onset will be more favourable to its establishment. Likewise the role of nitrogenous fertilizers will require study.

Finally, the place of the re-seeded pasture in the overall management system will become clearer as development work proceeds, and its place will be decided largely on the basis of its strategic contribution to the nutritional requirements of the system. In other words, re-seeding is regarded as a second step in the development of a pastoral system based on exploitation of the existing vegetation on the more fertile hill soils, rather than as an initiating step, and there are sound economic and topographical reasons why this should be so.

None of this work is short term, because the long-term implications of increased grazing pressure and pasture utilisation in respect of soil fertility and plant-animal-soil nutrient cycles can be expected to be substantial, particularly if significant vegetational changes accompany the expected improvement in soil fertility. These effects can be expected to be greatest on areas subject at present to low grazing pressures, e.g., areas dominated by *Nardus* and *Molinia*. Yet, because the dominance of these species in these areas arises from the fact that they are not favoured by the grazing sheep when alternatives are available, the desirable effects of intensive grazing would seem likely to be more difficult to achieve in practice in these areas. On the other hand, under controlled grazing conditions when alternative species are not readily available, *Nardus* and, particularly, *Molinia* appear to be readily eaten in the immature state which can only be maintained by intensive grazing.

It must not be supposed that benefits in terms of animal production will only accrue from intensification of pasture utilisation and of stock management over the whole area of hill farms. Clearly this is an unrealistic and perhaps unnecessary objective. Large areas of hill ground will continue to be used non-intensively; the elucidation of the principles on which pasture and soil management practices in these areas must rest will be a continuing problem, because the integration of their management with that of intensively-managed portions of the farm will allow more scope for positive management, even under non-intensive use, than is currently possible.

PUBLICATIONS

(*Reprints not available)

98. WANNOP, A. R. (1964). Scottish agriculture. (*Scot. Geog. Mag.* **80**, 90-98).

    A review of Scottish agriculture, under the headings of soil, topography and climate, types of farming, crops, farm livestock and agricultural output.

99. WANNOP, A. R. (1965). Hill farming tomorrow. (*Farming News Annual*).

*100. HEMINGWAY, R. G., RITCHIE, N. S., BROWN, NORA A. and PEART, J. N. (1965). Effects of grazing management on plasma calcium and magnesium concentrations of ewes in early lactation (*J. Agric. Sci.* **64**, 109-113).

    The effects of rotational grazing (twice weekly pasture change) and two systems of set-stocking on plasma Ca and Mg levels of lactating ewes were studied. Levels declined rapidly on first transfer to the experimental plots. Clinical grass tetany developed only in the presence of both hypocalcaemia and hypomagnesaemia; it did not occur in the high proportion of ewes which showed low plasma Mg values but which maintained normal plasma Ca concentrations.

101. GUNN, R. G. (1965). Levels of first winter feeding in relation to performance of Cheviot hill ewes. III. Tissue and joint development to 12 and 18 months of age (*J. Agric. Sci.* **64**, 311-321).

    Greater skeletal size was the most important and permanent result of improved winter feeding. This is discussed with regard to its desirability and assessment under hill conditions. Greater fat deposition, pelvic development and growth of the reproductive organs are also discussed with regard to possible improvement in lamb production during the first productive year.

*102. ROBERTSON, R. A. and DAVIES, G. E. (1965). Quantities of plant nutrients in heather ecosystems (*J. Appl. Ecol.* **2**, 211-219).

    The dry matter yields and the amounts of various plant nutrients in heather of different ages are considered in relation to the nutrient status of the soil and possible losses by burning. The estimated maximum loss of Ca, K, Mg, P and N by burning heather on a 10-year rotation is compared with inputs of these elements in precipitation.

103. ROBERTSON, R. A., NICHOLSON, I. A. and HUGHES, R. (1963). Runoff studies on a peat catchment. (Paper presented to the *International Peat Congress, Leningrad* 1963.) (This entry appeared as Reprint No. 94 in the Third Report; it has been renumbered and entered here as copies are now available.)

Data are presented on rainfall and run-off over 3 years. Direct estimates of potential evapotranspiration were made.

104. GRANT, SHEILA A. and HUNTER, R. F. (1966). The effects of frequency and season of clipping on the morphology, productivity and chemical composition of *Calluna vulgaris* (L) Hull (*New Phytol.* **65**, 125-133).

An experiment is described in which heather plants growing in boxes were clipped either in summer or in winter at different yearly frequencies. The effects of the treatments on morphology, productivity and chemical composition are described.

The view is put forward that the vigour of growth is dependent on the physiological age of the plant and that this is determined by the distribution of the dry matter among the leaf and current season's shoots, the older stems and wood, and roots.

It is suggested that a grazing intensity where approximately 60% of the current season's shoot length is removed should be the best form of moor management.

105. DONEY, J. M. (1966). Inbreeding depression in grazing Blackface sheep (*Anim. Prod.* **8**, 261-266).

Blackface rams were mated with a group of their own daughters and a similar number of non-related ewes. Female progeny from the matings entered the ewe flock unculled. Records of birth type, birth-weight, fleece and liveweights throughout life were obtained.

Inbred lambs had lower mean values for all measured characters than did their non-inbred half-sibs and there was a greater number of apparently barren ewes amongst the flock ewes which were expected to produce inbred lambs. The inbred progeny showed a higher incidence of barrenness and lower lamb survival rates at all ages than did their non-inbred contemporaries.

106. Doney, J. M. and Smith, W. F. (1966). Fleece characteristics of three strains of Scottish Blackface sheep (*Anim. Prod.* **8**, 313-320).

Fleece characteristics of three distinct strains of Scottish Blackface sheep were studied by sampling ewes of the Lanark, Galloway and Lewis strains on three occasions in a single year. During the period of maximum growth the Lewis strain differed significantly from the others in S/P ratio and mean weight, diameter and degree of medullation in fine and coarse fibres. The differences between the other two strains were small.

107. Doney, J. M. (1966). Breed differences in response of wool growth to annual nutritional and climatic cycles (*J. Agric. Sci.* **67**, 25-30).

Cheviot and $\frac{3}{4}$ Merino, $\frac{1}{4}$ Cheviot sheep were fed at similar annual maintenance levels. The annual ration was provided in three ways—in simulation of the 'natural' intake cycle, the reversed intake cycle or as a constant daily ration.

After an extended period of adjustment, the between sheep variation in intake, in the Merino group, was reflected in variation in wool-growth rate at all times. In the Cheviot group, intake and wool growth were related in summer but not in winter.

*108. Jenkins, R., Hurley, P. W. and Shorrocks, V. M. (1966). Plant mineral analysis by X-ray fluorescence spectrometry (*The Analyst* **91**, 395-397).

109. Russel, A. J. F. (1967). A note on goitre in lambs grazing rape (*Brassica napus*) (*Anim. Prod.* **9**, 131-133).

Thyroids of lambs grazing on rape were enlarged, compared with lambs on rape and receiving an iodine supplement or lambs grazing on aftermath. No differences were observed in rate of live-weight gain.

110. Russel, A. J. F. and Barton, R. A. (1967). Bone-muscle relationships in lamb and mutton carcasses (*J. Agric. Sci.* **68**, 187-190).

Carcass weight, bone weight, bone length, and bone weight per unit length were examined as possible indices of the weight of muscular tissue in lamb and mutton carcasses.

Carcass weight provided the best estimate of the weight of carcass muscular tissue in both lambs and mature sheep.

The level of prediction was improved by the use of

multiple regressions incorporating humerus weight as an independent variate with carcass weight.

111. RUSSEL, A. J. F., DONEY, J. M. and REID, R. L. (1967). The use of biochemical parameters in controlling nutritional state in pregnant ewes, and the effect of undernourishment during pregnancy on lamb birth-weight (*J. Agric. Sci.* **68**, 351-358).

An investigation of the use of plasma free fatty acid and ketone levels in the maintenance of prescribed levels of undernourishment in late pregnancy. Levels of undernourishment were maintained by weekly adjustments of feed intake in response to changes in the measured parameters. Moderate undernourishment reduced birth weights by 10%; severe undernourishment by 25%.

112. RUSSEL, A. J. F., DONEY, J. M., and REID, R. L. (1967). Energy requirements of the pregnant ewe (*J. Agric. Sci.* **68**, 359-363).

The additional nutrient requirement of the ewe in late pregnancy was estimated in two experiments as 100 g. D.O.M./kg. foetus/day.

113. PEART, J. N. (1967). The effect of different levels of nutrition during late pregnancy on the subsequent milk production of Blackface ewes and on the growth of their lambs (*J. Agric. Sci.* **68**, 365-371).

An investigation of the effect on subsequent milk production of three different levels of nutrition imposed during late pregnancy, with ewes fed ad libitum during lactation. Severe undernutrition in late pregnancy had no detectable effect on milk production of ewes rearing single lambs. Some effect was recorded in ewes with twins but it is suggested that any depression of actual milk production may be a result of an inability of the small twin lamb to exploit the milking potential of the ewe. Data on ad libitum feed intakes of ewes and lambs, and on growth rate of lambs, are presented.

114. GUNN, R. G. (1967). A note on hill ewe mortality (*Anim. Prod.* **9**, 263-264).

This paper presents records relating to some 1500 Blackface and 1000 Cheviot breeding ewes on three hill farms over a 10-year period (1955-1965). The mean yearly ewe mortality rate on all three farms was between 3 and 4%. Nearly 70% of deaths occurred during late pregnancy and early lactation (March to June).

115. EADIE, J. (1967). X International Grassland Congress, Helsinki. Review of Section 4—Improvement of grass production and utilisation on natural grassland in different climates (*J. Brit. Grassl. Soc.* **22**, 21-25).

116. DONEY, J. M. (1967). The effect of inbreeding on feed consumption and utilisation by sheep (*Anim. Prod.* **9**, 359-364).

This study was carried out to determine the relative importance of voluntary feed intake and efficiency of feed utilisation in the depression of growth rate shown by inbred sheep. When both inbred and outbred Blackface sheep were offered equal and restricted amounts of food the growth rates and gross efficiencies of food conversion for both body tissue and wool were not lower in the inbred group. When fed ad libitum the outbred sheep consumed 17% more feed and the daily rates of live-weight gain and wool growth were 33% and 27% higher, respectively. Since inbred lambs were smaller, the voluntary intake per unit live-weight did not differ between groups. Inbred sheep had a higher estimated requirement of feed for maintenance.

117. DONEY, J. M. and GRIFFITHS, J. G. (1967). Wool growth regulation by local skin cooling (*Anim. Prod.* **9**, 393-397).

Local cooling of the skin, produced by exposure to wind, was shown to depress the rate of length growth of wool. The depression was associated with reductions in skin temperature and blood flow and with increases in heat transfer in the exposed regions.

Papers accepted for publication

DONEY, J. M. Production of protein fibres (*Rev. Text. Prog.* **17**).

DONEY, J. M. and EADIE, J. The wool growth response to the annual cycle of grazing intake in Cheviot wethers (*J. Agric. Sci.*).

DONEY, J. M. and SMITH, W. F. Infertility in inbred ewes (*J. Reprod. Fertil.*).

GUNN, R. G. Levels of first winter feeding in relation to performance of Cheviot hill ewes. IV. Body growth and development from 18 months to maturity (*J. Agric. Sci.*).

GUNN, R. G. Levels of first winter feeding in relation to performance of Cheviot hill ewes. V. Dental development and persistence (*J. Agric. Sci.*).

PEART, J. N. Lactation studies with Blackface ewes and their lambs (*J. Agric. Sci.*).

REID, R. L. The physio-pathology of undernourishment in pregnant sheep, with particular reference to pregnancy toxaemia (*Adv. Vet. Sci.* **12**).

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