Institute of Terrestrial Ecology

Research in Scotland

Report for 1971-73

Natural Environment Research Council **50p net**

NATURAL ENVIRONMENT RESEARCH COUNCIL

INSTITUTE OF TERRESTRIAL ECOLOGY

RESEARCH IN SCOTLAND

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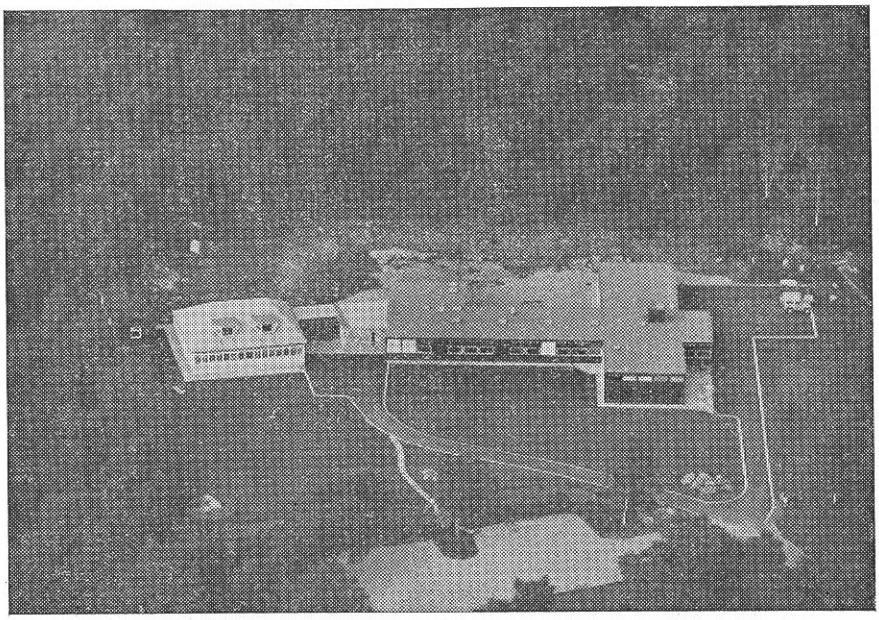
Institute of Terrestrial Ecology
Banchory Research Station
Hill of Brathens
Banchory
Kincardineshire
AB3 4BY



Brathens Research Station, Banchory, Kincardineshire.

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Introduction

D. Jenkins

This report for the period 1971–1973 follows the style of a previous report produced in this form by Nature Conservancy research staff in Scotland. However, during this period the research branch of the Nature Conservancy was replaced by the Institute of Terrestrial Ecology. This was created in autumn 1973 when the Nature Conservancy ceased to exist. The new Nature Conservancy Council came into existence on 1 November 1973 and the previously unified functions of management and research were divided between the two organisations. Thus, for most of the period covered, the staff whose work is described were employed by the Nature Conservancy, but for the last two months they were members of the new Institute and this report is produced by the Institute. The practice recently established by the Nature Conservancy of producing triennial reports will now be discontinued as the Institute will produce its own annual reports from the end of 1974. The wheel has gone full circle over six years since the triennial reports themselves replaced contributions formerly made in annual reports produced by the Nature Conservancy.

Organisation

The organisation of the Nature Conservancy in Scotland was described in the last report and did not change much in 1971–73. However, a new research station at Hill of Brathens, Glassel, Banchory was occupied in November 1972 and the Banchory research station is now one of the principal research stations of the ITE. In fact, there are two research offices in Banchory, one at Blackhall where research is done on red grouse and on some predators and the new station at Brathens, but they are both component parts of the same station. Staff at Blackhall include two scientists employed by the Department of Agriculture and Fisheries for Scotland working on foxes and supervised by D. Jenkins. Apart from these new developments, the organisation of research staff of ITE in Scotland is as described in the last report. An Assistant Regional Officer of the new Nature Conservancy Council is still based at Banchory, and the report includes an account of his work.

Brathens Research Station

Brathens Research Station is situated in 30 ha of birch woodland 4 km north of Banchory and 30 km west of Aberdeen. The building, a single storey system built construction, occupies 820 m^2 and is attached to an existing converted bungalow by a traditionally constructed spacious entrance hall. The accommodation includes offices, library, laboratories, oven room, cold store, a growth room and a seminar room to seat fifty persons. Mr R. R. Alexander of Messrs George Bennett Mitchell & Sons, Aberdeen, designed the building and it was built by Messrs D. C. Stewart (Aberdeen) Ltd. Work commenced in January 1972 and was completed by 1 November in the same

year. The cost was £80,000. Future plans provide for the construction of a botany complex of greenhouses and plant enclosure and an animal house.

Strategy

Staff based at Edinburgh were chiefly concerned with work on open waters and on peatlands. The main group of projects on the former concerned investigations at Loch Leven in connection with the International Biological Programme, and were organised in conjunction with other government research institutes and with universities. The theme was the investigation of energy flow through different trophic levels in a large fresh water lake. Nature Conservancy/ITE staff were chiefly concerned with the physical environment, phytoplankton, macrophytes, benthic fauna and with concluding and writing up earlier work on birds. Research on peatlands involved the survey and description of selected areas in relation to a review of the conservation value of these sites, and staff were also involved in compiling a bibliography and review of the British literature on peatland ecology

Research at Banchory is integrated in two main areas, vertebrate population ecology and upland ecology. Work on vertebrates includes basic research on red grouse, started in 1956 and now inquiring into increasingly fundamental problems of the inter-relations of population ecology, nutrition and behaviour. This work is extending into studies of other moorland birds of high interest to conservationists, especially waders such as golden plover, greenshank and dotterel. This focuses attention on different aspects of upland ecology. Another growth point is work on predator/prey relations including monitoring the numbers of eagles and peregrines. Studies continued on the behaviour and population dynamics of buzzards, on the importance of hen harriers as predators on red grouse and on the biology of sparrowhawks. These studies are also relevant to our interest in the effects of afforestation on upland wildlife. The work of the DAFS scientists based at Banchory was initially on likely effects on foxes and agriculture of the banning of the gin trap. Research on waterfowl mostly came to an end in the period except for small population studies on shelduck and mute swans. Some of this work is based on the Edinburgh office.

Work on upland ecology also includes studies of plant succession, and the impact of grazing animals and people on upland vegetation. The inter-relations of grazing animals and range pose major problems in many parts of the world and ecologists have an important role in offering advice on the effects of pressures from people and animals and the responses of vegetation. This work may lead to predictions for management in different circumstances from those under the present political and economic climate. An important theme in current work is understanding the constraints imposed on upland systems by existing management and the successions and inter-relations that might develop if these constraints were modified. In what ways do grazing pressures influence botanical changes in moorland, and what advice can ecologists give on the densities of grazing animals that may produce or influence changes in desired directions? Zoologists have worked together with botanists in the Range Ecology Group, and studies of the behaviour and ecology of red deer have continued. Red deer are the major wild grazing mammal in this environment.

New work started on puffins. This sea-bird is undergoing a major decline in numbers in the very large colonies on islands in the west of Scotland. This

new development follows a gradual retraction of distribution in the southern part of the range of this species, and the work aims to find the reasons for the decline.

Staff

The total staff of ITE in Scotland in December 1973 was 52 with 18 at Edinburgh Headquarters, 6 at Blackhall and 28 at Hill of Brathens. Of these, 42 are engaged on research and 10 on administration. The structure of the staff is shown below. The research groups and their heads are as follows:

Grouse	Dr A. Watson
Range Ecology	Mr I. A. Nicholson
Wetlands	Dr P. S. Maitland
Vertebrate populations	Dr D. Jenkins

The tradition of research students working with permanent staff has been maintained and there were four at Edinburgh and four at Banchory. The work of some of these people is described in this report.

Changes in research staff in the period of this report were as follows:

Appointments

Miss J. M. Crisp	Scientific Officer, 11 October 1971
D. King	Scientific Officer, 18 October 1971
R. Britton	Scientific Officer, 1 July 1972
Miss M. E. Bindloss	Scientific Officer, 1 January 1972
P. W. McDonald	Scientific Officer, 17 April 1972
M. P. Harris	Senior Scientific Officer, 3 July 1972
L. C. MacRae	Deer Stalker, 1 September 1972
D. C. Watt	Assistant Scientific Officer, 15 October 1973
Miss C. M. Cran	Assistant Scientific Officer, 15 October 1973
Mrs L. E. Britton	Assistant Scientific Officer, 1 April 1973
A. A. Lyle	Assistant Scientific Officer, 24 April 1973
K. H. Morris	Assistant Scientific Officer, 23 April 1973

Resignations and retirements

A. B. McLennan	Assistant Experimental Officer, 16 April 1971
Miss M. C. Gray	Higher Scientific Officer, 30 November 1971
Miss W. J. Jenkins	Assistant Scientific Officer, 7 January 1972
D. J. McLennan	Deer Stalker, 29 February 1972
D. King	Scientific Officer, 15 June 1973
E. A. Kemp	Assistant Scientific Officer, 27 July 1973
Mrs A. Miles	Assistant Scientific Officer, 16 February 1973
P. McRae	Deer Stalker, 28 February 1973

Professor D. A. Boag (University of Alberta) spent a sabbatical year in 1970–71 with the Grouse Team, and in 1972 Professor C. D. MacInnes from the University of Western Ontario worked about 4–5 months at Blackhall. In 1972, Dr Watson gave a course on population in birds at the University of Lund and visited north Norway to see research on willow grouse and lemmings. He also attended the Public Enquiry on the Cairn Gorm disaster for a week as an expert witness. Dr Mitchell attended congresses of the International Union of Game Biologists in Paris and Stockholm in 1971 and

1973. Dr Moss was one of the principal speakers at this Stockholm meeting which was also attended by Mr Hewson. In autumn 1973, Dr Mitchell received a Nuffield Fellowship which enabled him to travel extensively in Europe and to visit New Zealand. Several members of the Wetlands Team were abroad at IBP meetings in Austria and Sweden and Dr Bailey-Watts visited Leningrad. Mr Nicholson also visited the USSR for three weeks in 1971 under arrangements made by the British Council, Dr Goode attended the Fourth International Peat Congress in Finland in 1972 and Dr Maitland was in Canada in 1971 and in Norway in 1972. In addition, Mr Smith visited the Lake George IBP Research Centre in Uganda. Dr Miller attended a conference on fire ecology in Florida in 1973 as a guest of the Tall Timbers Research Station. A large number of visiting scientists were welcomed at all three research centres. These included Mr Donald Chisha, a FAO Fellow from the Department of Wildlife and Fisheries in Zambia, who was at Banchory from March to September 1973. Mr Chisha was tragically killed in a car crash soon after his return to Zambia. Professor R. T. Ogilvie from the University of Calgary worked with the Range Ecology Group on montane vegetation, and Mr G. Wiersema a student from the Agricultural University, Wageningen is currently at Banchory for a year studying red deer and seabirds. Mr P. Lugge is also spending a year as a sandwich student, working with Dr Bayfield and Mr Forster.

Dr Watson was awarded a grant of £240 by the Carnegie Trust for the Universities of Scotland, for field research on Gaelic place names in the Cairngorms and upper Deeside.

This report

This section outlines some of the main results in 1970–73 and growth points for the future.

A new project where the Grouse Team measured the quantity, chemical composition and growth of heather in the spring, confirms an earlier hypothesis that maternal nutrition affects subsequent breeding success. An intensive study of social behaviour and inheritance of wild grouse shows that territory ownership is largely a family affair, with young cocks contesting for their father's territory and often evicting him. Research with captive grouse indicates that their dominance and aggression are not usually correlated, and that differences in the behaviour that is involved in the peck order are inherited.

For the Wetlands Research Group, the International IBP/PF meeting at Reading in September 1972 represented the final comparative meeting at which all the PF sites, including Loch Leven, could be studied and discussed. A comprehensive data report of the Loch Leven results was made available at this meeting. The levels of production achieved at Loch Leven are among the highest from any natural fresh water. In June 1973 a highly successful symposium devoted to the Loch Leven IBP Project was held at the University of Stirling and attended by some 200 scientists from 15 countries. The 25 papers presented at this symposium will be published during 1974 by the Royal Society of Edinburgh. Work in the field of peatlands is proceeding well and it is hoped that the present project will culminate in a monograph on British peatlands published about 1976. The Group has continued to give

advice on wetland management problems to a wide range of organisations and individuals throughout Britain.

Work on predators, especially birds of prey and foxes, has extended along the lines outlined in the previous report. Toxic pesticides and gamekeepers continue to have an important effect on the numbers of raptors, making it difficult to understand natural processes. However, sparrowhawks are increasing in some parts of Scotland, especially in Forestry Commission woods where the numbers of birds of many kinds are now known to be higher than was sometimes thought. Studies of prey are a growth point for the future in relation not only to conserving predators but also to understanding the effects on wildlife of changes in land use. Voles and sheep, as carrion, are usually key species in the uplands. Studies of predators and their prey remain an important focus for research oriented towards conservation.

Most studies begun in Range Ecology when the Group was established in 1968 have now been completed and are being written up. Much attention has been given to problems of vegetation stability and succession and the role of animals in controlling trends. Over large areas of upland range the only practical way of exercising positive ecological control may well be by understanding how to foster successional development towards scrub or woodland. This field of research has been increasingly emphasised. Because of the particular importance of birch as a successional species in a variety of situations and its possible role in soil development, it has received special attention. New work on red deer has contributed greatly to understanding the factors affecting their growth and reproduction and their influence on population processes. Research on montane ecology has also been started. This is a comparatively neglected field which offers great scope for understanding fundamental problems of plant establishment, growth and succession under severe physical conditions, and in circumstances where human pressures are increasingly presenting urgent management problems. In addition to ecological research over the past three years, members of the Group have also been heavily committed to a variety of management problems on nature reserves, including management planning.

Grouse Research Group

A. Watson

1. Introduction

In 1971–73, the team's main emphasis continued on a fundamental study of population limitation in red grouse. Much of this involves detailed work on social behaviour, nutrition and inheritance, and the two Ph.D. projects contribute to this. The lease was renewed at Kerloch moor so that the team could carry on this research. With greater affluence among shooters and with better management of heather moors, grouse shootings have greatly increased in value. It is now very difficult to find areas for research on grouse which are not subjected to high shooting pressure, intensive heather management, and considerable limitations on what the researcher can do. Retention of the Kerloch lease allows the team to do a detailed study of an unshot population on a part of the moor where no intensive heather management is practised, and also to do experiments that would not be possible elsewhere.

The central idea in this work continues to be that population density is determined by the territory size taken by the cocks in autumn. Much of the work is aimed at elucidating factors which influence territory size. We are particularly interested in the birds' agonistic behaviour, which has been shown to be a major determinant of territory size. Factors affecting agonistic behaviour and territory size can be classified into pre-hatching effects such as maternal nutrition and genetic constitution, and post-hatching effects such as those due to the physical structure of the environment and nutrition after hatching. Another field project is to follow the family history of several generations of cocks, to see if their ability to get a territory and the size of territories that they take are affected by inheritance. In captivity, a detailed study of the inheritance of dominance and aggression is being done.

A small amount of applied work on grouse and moor management continues, in co-operation with other organisations. One of the new projects is to find if stocks of grouse can be increased in the very barren habitat of western Scotland, by changing the management of the heather. Another is to study the possibility that ticks affect the breeding success of grouse.

In 1971–73 the team increased its work on other species. R. Moss began studying the rare greenshanks of upper Deeside in 1970, and in 1973 R. Parr started detailed research on golden plovers at Kerloch. A. Watson continued long-term monitoring of the populations of eagles, peregrines, dotterel and other hill birds in relation to human impact, and also did more detailed work on numbers and breeding success of dotterel.

2. Red Grouse Populations

The aims of the population studies are to understand more about the processes by which numbers change and to act as a necessary background to the work on social behaviour and nutrition. During 1971–73 the stocks of breeding grouse reached extremely high densities on Kerloch, following several mild winters and springs with subsequent good breeding success. Densities reached levels of about one territory per ha over large areas. Ground with poor management of heather also had high stocks and breeding success,

but population densities were lower than on the better-managed parts. During this period, an experiment with nitrogen fertilizer showed that birds did not rear larger broods than on unfertilized ground, where breeding success was extremely high anyway. This contrasted with an earlier experiment where fertilizer did increase breeding success and breeding stocks, but numbers were generally low then. During the current experiment, in one year sufficient territorial cocks on the fertilized area were bigamous to raise the sex ratio to about 1·5 hens per cock. Sex ratios of breeding grouse populations are usually 1 : 1 or show an excess of cocks, but the new finding shows that the population density of breeding hens does not necessarily depend merely on the number of territorial cocks.

(*A. Watson, R. A. Parr, R. Moss*)

3. Behaviour of Wild Grouse

The main project here involves marking all the chicks on a large area and studying what happens to them later. We are interested in the role of inheritance and type of bird in causing variations in territory size, social behaviour, population density, and in contributing to the gene pool of future breeders. Results confirm earlier suggestions that ownership of the same ground over a period of years is held mainly within the family. Young cocks each autumn challenge their own fathers, uncles and brothers, and often evict their close older relatives. Hens disperse much more, and may settle with cocks some distance from where they were hatched. This work is also providing evidence on variations in territory size and social behaviour in relation to fluctuations in population density over several years.

(*A. Watson, R. A. Parr*)

4. Effect of Radio Transmitters on the Behaviour of Red Grouse

Much research has been done using radio telemetry to study the behaviour and movements of wild animals. However, a crucial question with any such technique is whether it affects the results obtained. In the case of telemetry with wild animals, little checking of this has been done. In 1970–71, Prof. D. A. Boag from the University of Alberta spent a year at Blackhall, studying this problem in red grouse. He measured activity, food intake and use of different kinds of artificial cover by captive birds which he had fitted with radio transmitters. The grouse carrying the transmitters were less active than control birds, and hens with radios ate less than control hens. There was no difference in their use of cover. The differences in activity and food were greatest in the first week after radios were fitted. Prof. Boag also did a study on wild grouse, in co-operation with A. Watson and R. Parr. Wild birds were fitted with dummy radios and released, and their subsequent performance followed. The survival and the territory size of birds with dummy radios were no lower than in birds without them. Thus, despite the differences of behaviour noted in captivity, there was no evidence that the long-term performance of wild birds was affected. Both studies have been published.

5. Nutrition and Breeding Performance in Individual Red Grouse

Field work for this study ended in spring 1971. One of the main ideas in the grouse work at the moment is that populations of grouse breed better in

years when the hens, on average, have better food before egg-laying. My main aim was to find if differences in the food available to individual hens on their territories could explain some of the variation in their subsequent breeding success. The main conclusion was that the nitrogen content of the heather on a hen's territory in any one year was related to her ensuing breeding success.

(*A. N. Lance, Ph.D. Student*)

6. A Comparison of Genetics and Behaviour in a High and Low-Density Population of Red Grouse

This Ph.D. study began in late autumn 1972. The two main questions are: (*a*) Do red grouse from high and low-density populations differ genetically? (*b*) Is the dominance rank of captive cocks correlated with the genetic markers which are used to distinguish high and low-density populations? The populations are on two moorland areas, each of approximately 60 ha and lying 5–7 km apart at opposite ends of Kerloch moor. The biochemical genetic marker is a plasma esterase, probably the same as Redfield (1972: Ph.D. Thesis, University of British Columbia) used in his study of blue grouse. The data are being obtained by electrophoresis of plasma in samples of blood taken from chicks and adults, captive and wild. New morphological genetic markers, based on plumage pigmentation and down colour, have been found for the genetic comparison. Dark, intermediate and light morphs are being used with the adults and black, brown and yellow down in chicks.

(*B. Henderson, Ph.D. Student*)

7. Nutrition and Maternal Inheritance in Relation to Grouse Populations and Social Behaviour

Studies on captive birds are being done, with the aim of discovering the role of inherited factors in determining the aggression and dominance of an individual. We are trying to distinguish between genetic and non-genetic inherited effects; and we are also now beginning to make a clear distinction between aggression and dominance, which are not usually correlated. This work is being done in parallel with population studies on wild birds, from which samples of eggs are taken each year. Our main idea at the moment is that the nutrition of the hen affects the agonistic behaviour of her offspring and hence their territory size and subsequent breeding densities.

We now have better evidence confirming the old hypothesis that maternal nutrition affects the breeding success of grouse. This comes from a project where we measured the quantity, nutrient content and growth rate of heather in the spring, and compared them with subsequent breeding success. In warm springs, the heather grew early and grouse bred well that summer. Also, the more heather that was available to hen grouse when they were laying their eggs, the better the chicks survived. In turn, breeding success was related to changes in breeding densities: following good breeding, numbers of breeding birds in the following spring tended to increase and vice versa.

(*R. Moss, A. Watson, R. A. Parr*)

8. The Effects of Post-Hatching Nutrition on the Behaviour of Red Grouse in Captivity

This 3-year Ph.D. study with captive grouse ended in late 1973. It originated from some observations on wild grouse which suggested that the aggressiveness and territory size of cocks was influenced by the nutritive value of their food when they grew up as chicks.

In captivity, chicks were put on high and low-protein diets which produced groups of birds with high and low growth rates. Once they had become adult, measurements were then made of their aggression (that is, their tendency to attack a standard stimulus) and of their dominance in a group hierarchy; these two measures were not correlated. The results were not in the predicted direction: in fact, the chicks reared on the high-protein diet were more dominant. However, this result was obtained when all birds were ranked while on a high-protein diet. When both sets of grouse were subsequently put on a low-protein diet, some birds changed their rank: the birds which had grown up on the high-protein diet now tended to be less dominant. This raises the possibility that birds will perform most successfully when their nutrition is similar to that which they experienced while they were growing.

(M. Marquiss, Ph.D. Student)

9. Applied Work on Grouse

Phosphorus fertilizer was spread from the air on two moors in Morayshire in spring 1970, the fertilizer and its application being paid for by the estate. This increased the phosphorus content of the heather. The red grouse then bred slightly better and breeding stocks increased relative to the control area, but the improvement was patchy, not occurring on every fertilized area in every year. The areas were open to sheep grazing. Fertilizing on ground open to sheep is unlikely to be of much economic value for the grouse shootings alone.

A joint project has been started on Mull in co-operation with the Highlands and Islands Development Board and John Phillips. The main aim is to find if grouse numbers can be increased to a level that would make shooting worth while. We think that the potential for grouse is fairly good over much of Mull, although the present numbers are extremely low (less than one pair per 40 ha). Current management, which is for sheep, involves burning very large areas at a time (frequently over 50 ha). Preliminary work has been done in preparation for experiments which will change the management on small study areas.

In much of Morayshire, ticks have been common for many years and are blamed there for low grouse stocks. In summer 1973 a co-operative research project on this began on a Speyside moor, paid by a private estate. John Phillips is in charge of organisation and he and James Duncan are doing most of the field work, with the grouse team involved in the experimental design and interpretation and in a little field work. During the summer, Hugh Reid of the Moredun Institute at Edinburgh also joined the group; he is studying 'louping-ill', the common tick-borne disease of sheep, and its transmission by the wild mammals and birds that carry it.

(A. Watson, R. Moss, R. A. Parr)

10. Grouse in Ireland

Our co-operative work with P. J. O'Hare of the Agricultural Institute in Co. Mayo, western Ireland, ended in August, 1971. It was decided in 1970 that our exploratory study, based largely on two visits in April and August each year, should be followed up by full-time work. A. N. Lance, who had previously been a Ph.D. student with the grouse team was appointed to the post in May 1971. The aim of our work had been to find if grouse numbers could be increased in this very wet infertile habitat of deep blanket bog, where grouse are very scarce (less than a pair per 40 ha). The experiments that we began in 1968–69, involving fertilizing and keeping out sheep, continued in 1971 to show that numbers of grouse can be greatly increased by such treatments. Thanks are due to the Irish Department of Lands whose grant made our work possible.

(*A. Watson, R. A. Parr*)

11. Nutrition of other Tetraonids

Studies on the digestion of natural foods by grouse and ptarmigan have shown that tetraonids digest cellulose and lignin, probably in their very long caeca. Also, uric acid is not the main end-product of nitrogen metabolism as is the case in chickens. At low protein intakes, tetraonids produce more ammonium salts than uric acid, and may also produce ornithuric acid when eating certain foods.

The use of magnesium as a digestibility marker has been used to study food intake and digestibility in both wild and captive tetraonids. This technique was used to study ptarmigan in Alaska, where R. Moss spent the year 1969–1970 at the University of Alaska. The results showed that the energy intake of wild rock ptarmigan was only about 1·5 times their resting metabolic rate as determined by G. C. West (1972: *Comp. Biochem. Physiol. 42*, 867–76).

Gut length in tetraonids seems to be related to diet. Captive red grouse, fed on a pelleted diet, have much shorter guts than wild birds. Hence the results of studies of nutrition on captive birds may not be directly applicable to the wild.

(*R. Moss*)

12. Ptarmigan Populations and Behaviour

The main interest here has been to study populations and behaviour in a fairly natural habitat and to compare results with the more intensive studies of red grouse on managed ground. The work on ptarmigan is done on hills in north-east Scotland from about 750–1,200 m above sea level. The data confirm earlier suggestions of a long-term ten-year cycle in this area. Numbers reached a peak in the Cairngorms massif during 1971–72, higher than had been seen there in the previous two decades. The high spring populations there followed a summer of very good breeding success in 1970, after several years of low numbers. At the Cairnwell, we ascribe poor breeding in 1971 to crows eating the birds' eggs. In 1971 and 1972, breeding failed on the highest plateaux after heavy June snowstorms. The mean breeding density and breeding success of stocks at the Cairnwell have remained higher than in the Cairngorms for about ten years. This is associated with a difference in the underlying rock (lime-rich schist at the Cairnwell, acidic granite in the Cairngorms) and in the chemical composition of the birds' food plants.

The habit of ptarmigan and other hill species, of burrowing into snow for shelter during winter, is being studied by A. Watson in the Cairngorms area, in relation to problems of human survival in the hills.

(*A. Watson, R. Moss*)

13. Hill Wading Birds

Wading birds are an attractive and interesting part of the upland fauna, and we have recently increased work on them. The most intensive study is on golden plovers at Kerloch, started in 1973 by R. Parr. This is a species which is probably sensitive to differences in upland fertility and changes in land use. In 1973, all birds on the moor and in the nearby fields were counted at regular intervals in the spring and summer, and observations made on their behaviour and habitat. As many nests as possible were found and data were obtained on clutch size and hatching. Most chicks were colour-ringed in the nest and their progress was then followed subsequently.

The breeding density and success of a few pairs of greenshank in part of upper Deeside have been checked by R. Moss since 1971. The interest here is that these birds are at the edge of the species' breeding range, and this exploratory study might provide some clues about what limits this range.

Since 1971, A. Watson has made detailed observations on numbers and breeding of dotterel in the Cairngorms region. Breeding success is being studied in relation to habitat type, time of the birds' arrival and departure, and the effects of June snowstorms on first clutches.

(*R. A. Parr, R. Moss, A. Watson*)

14. Human Impact on Hill Birds

Long-term monitoring was continued on the breeding stocks and breeding success of red grouse, ptarmigan and dotterel in the Cairngorms region. The work is done on areas where there is heavy human disturbance near ski lifts at Cairngorm and the Cairnwell, and on nearby areas where very few people go. The data for all three species continue to show no obvious difference in stocks or breeding success on disturbed and undisturbed ground. At the Cairnwell, grouse stocks reached extremely high densities and grouse also increased at Cairngorm. Dotterel stocks remained very stable from year to year, on disturbed and undisturbed areas. These studies also involve counts of people on all the areas and on other hills. The counts are showing enormous differences (>100-fold) in numbers of people on hills near and away from chair lifts.

(*A. Watson*)

15. Birds of Prey

Long-term monitoring was continued on the populations and breeding success of golden eagle and peregrine in Deeside and north Angus and Perth, and the sample was extended due to the participation of A. Payne. These inland peregrines have continued to breed well. Over the three years, 26 successful pairs whose young were counted reared young and only a few pairs had their eggs robbed or failed for other reasons. In addition two entirely new pairs became established in the area. Eagles also continued to do well in the central high-lying part of the region, where 13 pairs reared 40

young over the three years. In the more outlying parts most birds failed to rear young, in some cases due to human interference. Eight outlying home ranges produced only three fledged young over the three years. Nevertheless, there was encouraging evidence of three pairs beginning to establish again in ranges that were vacated after human interference in the 1940s and 1950s and had stayed vacant since.

(A. Watson)

16. MOUNTAIN HARES

This M.Sc. study ended in 1973. It comprised a re-analysis of earlier data from a population study of mountain hares in Banffshire and a new investigation of food selection in Deeside during 1970–73. The population study from 1956 to 1969 showed that numbers increased from 1956–58, went down in 1959, and stayed low until 1966. Another increase began in 1967. When there were few hares they bred more successfully and survived better. Good breeding in 1967, coupled with unusually good survival until at least 1969, may have started the increase leading to the next peak.

Counts of droppings from sample plots showed that the hares selected those with mostly short young heather. Heather samples taken at those plots did not contain more N and P than on other plots, so that selection on them was based on the height of heather rather than its nutritive value. Further work on this aspect is being done with brown hares grazing on trial plots of farm crops.

The stomachs of mountain hares contained more N and P in autumn than in spring, and in March the stomachs of females contained more N and P than those of males. Feeding trials with captive mountain hares showed no clear-cut selection between different moorland plants, ages of heather, or fertilized as against unfertilized heather. Among moorland trees, willow and rowan were most eaten and birch least.

(R. Hewson, M.Sc. Student)

Range Ecology Research Group

I. A. Nicholson

1. Introduction

Most of the projects begun in 1969, after the Range Ecology Group was set up, have now been completed. Much of the period since the last report was published in 1970 has been occupied in concluding and writing up this first series of studies, though new work has been planned and part of this programme has already started.

The original objectives in bringing staff from different disciplines together in one research unit were, first, to promote a more cohesive approach to range problems involving interactions between grazing animals and vegetation; and second, to meet existing commitments of the Nature Conservancy in the area of management and to do research to underpin the work of the Conservation Branch over a broad field. These latter requirements involved immediate demands relating to many *ad hoc* problems of reserve management, red deer management, and recreation. It was therefore essential to arrange the programme to maximise the opportunities for research in depth to promote understanding of some of the underlying ecological problems of upland and mountain range.

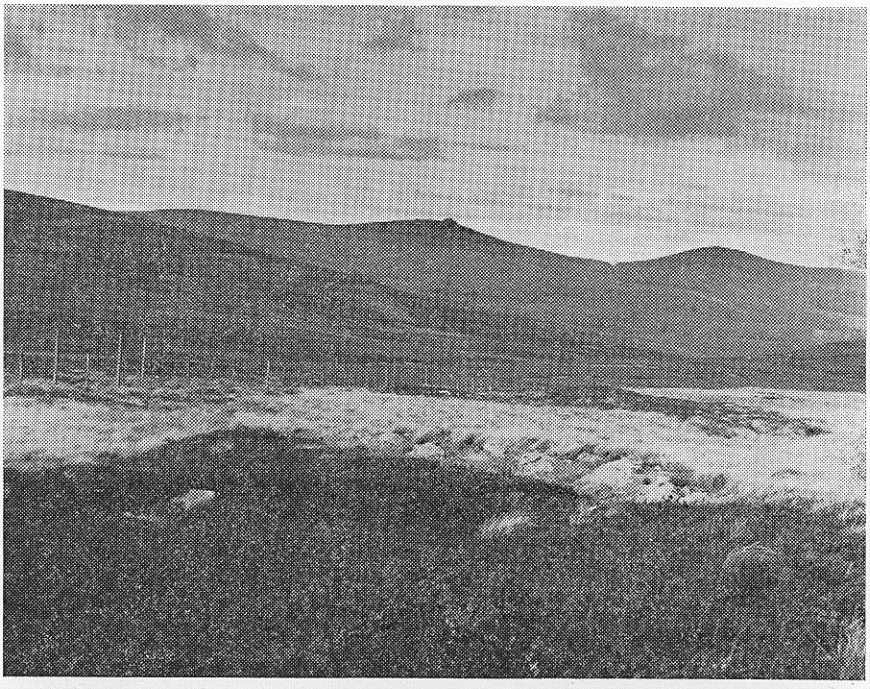
Problems in the dynamics of vegetation and the factors affecting stability and successional change, particularly in relation to the influence of grazing animals, were recognised as a neglected field. Moreover, many issues affecting reserve management were directly related to problems of this kind. A number were also associated with the red deer as an animal of high resource value and at the same time a widespread source of pressure on Highland vegetation. The main research effort was therefore concentrated in this field of animal/grazing interactions. It was also recognised that ecological problems in the high mountain areas required special consideration. However, resources were inadequate to enable all this to be developed at once.

Two of the main commitments involved the Island of Rhum, a National Nature Reserve owned by the Conservancy, and Glen Feshie estate, a 17,400 ha deer forest in the Cairngorms, much of which lies within the boundary of the Cairngorms National Nature Reserve. An arrangement that had been made with the proprietors provided for the use of the estate as a research area. It also involved participation in the development and management of the estate, including that part covered by the Reserve Agreement. The work on this estate was therefore of two kinds. First, it involved a series of descriptive studies to provide a basis for development recommendations and to establish a system of surveillance covering certain characteristics of the vegetation and the red deer population. Second, the area was used as appropriate in connection with the development of the main research programme. The development work was maintained largely as a separate activity from the use of the estate for this purpose. However, some studies including population work on red deer and work on woodlands have served a joint purpose. For example, the woodlands offered a valuable opportunity to describe the sequence of depletion in a representative area of the Cairngorm mountains, while studies on regeneration in relation to grazing have been

continued as a research project. Many of the projects outlined in this and the previous report were done using the facilities of Glen Feshie and those of the Island of Rhum.

Studies on heather (*Calluna vulgaris*) moorland in north-east Scotland have drawn attention to the importance of species poverty and soil characteristics, to some extent created by the growth of heather itself. These features contribute to the stability of this type of vegetation. Similar problems occur on range dominated by *Molinia* and these are also being investigated. Problems in the establishment of birch (*Betula spp.*) and the role of this species in changing site conditions in heather-dominated communities are now being examined. Indeed problems of birch ecology have been given some emphasis in successional studies. A great deal of work has been done in the past on the effects of burning, but little attention has been given to either the problem of establishing vegetation 'higher' in the successional sequence that does not burn readily, or to the ecological consequence of this to site conditions, including the soil and floristic properties.

Factors affecting the establishment of a variety of shrubs and trees have also been studied, with special reference to the impact of grazing animals. Under the conditions of one investigation it is already clear that significant variation can occur in the liability to damage according to elevation, a markedly lower incidence of damage occurring towards the higher levels within the tree line. In collaboration with Dr Floate of the Hill Farming Research Organisation, the long term effects of different regimes of grazing and burning on the soils and vegetation of sites that were evidently uniform



A typical area of heather (*Calluna vulgaris*) dominated range in north-east Scotland used for red deer, sheep and red grouse.

at an earlier time, have been investigated using fenceline situations. This work has drawn attention to some of the positive aspects of heavy grazing on certain soils in bringing about an increased rate of nutrient turnover. It has helped to establish a more balanced view of the role of grazing, the degenerative effects of which are often emphasised in the ecological literature. A long term study of the effects of grazing by wild and domestic animals on various kinds of vegetation in north-east Scotland is still in progress. A tentative interpretation of grazing influence using some of the data is discussed in this report.

Studies on the effects of pressure on vegetation have included research related to recreation. A number of reports of investigations in specific areas notably the Cairngorms and the Pennines have already been published. Consumer demand in the recreational field for information has been considerable, but as in the case of red deer work the need for research at a more fundamental level has been emphasised.

The earlier work on red deer in the Nature Conservancy was mainly concerned with the dynamics of populations. This work raised many issues about the factors influencing the underlying processes of growth, reproduction and mortality, and their relationship to range conditions in terms of nutrition, shelter and topography. The research was therefore reorientated with the aim of understanding these processes. One of the first requirements was to obtain more precise information about the characteristics of red deer of different age and sex throughout the annual cycle. A detailed study was done on Rhum over a two-year period. We now have reliable data from one habitat on seasonal changes in weight and condition, and some information on changes in morphology and physiology. This has already assisted greatly in interpreting a number of observed features of population performance. Experimental studies on nutrition were also done by a member of staff at the Rowett Research Institute, an arrangement made possible by the generous co-operation of the Director, Dr K. L. Blaxter and of the Head of the Physiology department, Dr R. N. B. Kay who supervised the work.

Research over the past five years has clarified a number of problems of vegetation dynamics and the role of the larger grazing animals, especially the red deer. Some important fields for further investigation have been identified. Moreover, a much sounder basis for understanding many management problems has already been established. In the case of the red deer it is now possible to take a much more balanced view of the ecology of this animal, and hence of the whole question of management control in deer/range systems. Problems in this field have recently been reviewed (*Mammal Review*, in press).

2. The Stability of Heather Moorland

Two-thirds of the land area of Scotland is classified by the Department of Agriculture and Fisheries for Scotland as 'rough grazings'. This is mostly plagioclimax vegetation that has developed since Neolithic times following progressive destruction of the natural tree cover, with subsequent burning and grazing over a long period. Heather is the most abundant plant over large areas, while *Calluna*-dominant vegetation (Callunetum), popularly called heather moorland in the uplands, is widespread, particularly in the central and eastern Highlands.

Today, most heather moorland exhibits a marked stability. This is partly because heather is so well fitted to the moorland conditions. It grows better than most non-arboreal species in the generally acid and infertile soils. It also quickly regenerates a new canopy after fire, thus maintaining its dominance. Current burning and grazing practices tend to prevent reinvasion of the ground by trees, and, except at high altitudes, are probably the primary factors causing stability. However, even when not burnt or grazed, most moors revert to woodland very slowly, indicating that other factors also induce stability. Our understanding of these has been clarified by experimental studies, now largely completed, on several moors in the north-east, central and north-west Highlands.

Species poverty

One feature contributing greatly to stability is the general lack of seed of successional species, and of certain tree species in particular, that can invade and then change moorland. This is due to the large area and floristic poverty of most moors, including the absence of successional species present as buried seed. In the absence of seed of other species, heather-dominant swards tend simply to be regenerated after destruction of the canopy, whether by fire or other agents, although this may not happen if fire is too frequent, burns far into the surface organic matter or is followed by erosion or heavy grazing, or if the sward was already changing when the canopy was destroyed. Thus, when ground was bared experimentally at three different heather moor sites in north-east Scotland, it was found that recolonisation tended towards the direct regeneration of the surrounding vegetation. Also, when seed of 107 species was sown on bared soil at the same sites, from 28–67 per cent. of the species established, indicating that many more species can establish at the sites than grow there at present. These new species included many that may have been present at the sites under former woodland conditions.

Soil infertility

The infertility of most moorland soils is another important cause of stability. This infertility has resulted partly from base-poor soil parent materials, and partly from the effects of the heather itself on the soil. Nutrient deficiencies and aluminium toxicity induced by acidity prevent many species from growing. Thus, in the experiment where natural recolonisation was studied, only one species of flowering plant that was not already present in the surrounding vegetation appeared and established on unfertilized ground. In contrast, on ground that had been given a dressing of fertilizer, a total of ten new species, mainly ruderals, and of no successional significance, established at the different sites from seeds that had been dispersed there naturally. Also, in the experiment in which seed of 107 species was sown in, from 68–86 per cent. of the species established on fertilized ground, many more than on unfertilized ground. These also included several that may have been present under former woodland conditions.

Effects of the vegetation

Previous studies have shown that seedlings tend to establish very poorly within undisturbed heather swards, whether from naturally sown or experimentally sown seed. This was investigated by sowing seed at four

different sites following successive removal of different layers of the vegetation and examining establishment. The results indicate that both the structure of stands of heather-dominated vegetation and the size of any openings that may appear also influence the likelihood of establishment of new species entering as seed. At two of four sites studied, both the heather canopy and the ground layer of mosses and lichens had a considerable effect on early establishment, though this was less at the other two sites. At all four sites, the litter layer and the adjacent 2–3 cm of surface organic matter inhibited early establishment considerably, and more than the combined effects of the heather canopy or ground layer. This effect of the surface organic matter might be a function of its infertility and perhaps also or the factor of factors toxic to mycorrhizal fungi recently demonstrated elsewhere to be present in the raw humus under heather.

The rapidity of vegetative regeneration also influences stability. When different sized patches of ground were bared experimentally in a species-rich heather-dominant sward on a brown forest soil, the density of self-sown seedlings of most species was much greater in 25 cm^2 patches than in 250 or 2,500 cm^2 patches, the increase varying up to 4,800 per cent. However, mortality in the smallest patches was so high, apparently as a result of competition from vegetatively regenerating plants spreading in from the edges, that few seedlings were still living after three growing seasons. This resulted in only 6 per cent. of the total new cover after three growing seasons in 25 cm^2 patches being derived from plants regenerated from seed, compared with 51 per cent. in 2,500 cm^2 patches. It thus appears that small openings in the vegetation, such as can be created by animal hooves kicking out or turning over small sods, or by the death of certain plants, may rarely permit the entry of new species from seed because of their very short duration. At least at the brown forest soil site, small seedlings probably have a good chance of surviving to maturity in larger disturbed patches only, such as are caused by moles (*Talpa europaea*); but moles occur on few heather moor sites.

Seed predation

Seed predation is probably a further cause of stability. Thus when Scots pine (*Pinus sylvestris*) seed was sown on five different heather moors, up to 100 per cent. losses were attributed to predation by woodmice (*Apodemus sylvaticus*), bank voles (*Clethrionomys glareolus*) or other predators in two successive years. Four of these moors were so distant from the nearest seed-bearing pine trees that only the occasional seed would ever fall there. With the losses found experimentally, such seeds could rarely be expected to remain intact long enough to germinate, and this might well apply to incoming seed of other species also.

Conclusions

There are many factors, usually interacting, that determine the pronounced stability shown by most heather moors. Their relative importance varies from site to site. They will also vary in time, especially as the structure of the vegetation changes with different phases of the life cycle of heather, coupled

with climatic fluctuation, and as seed predation changes with fluctuations in population size of predators. However, it is now possible to view more comprehensively than before the many factors governing the stability of heather moorland, and hence also governing the ease with which they can undergo successional change.

(*J. Miles, A. M. Miles*)

3. The Effects of Birch on Soils and Vegetation

Little is known of the effects that dominant plant species have on their environment. However, this is clearly central to the advancement of both basic ecological understanding and its application in ecological prediction and environmental management. In particular, the reputation of birch (*Betula pendula* and *B. pubescens*) for soil improvement has, if true, profound implications for the use of the uplands, where there is widespread soil degradation resulting from past use, and a correspondingly depleted flora over large areas.

Probably the most abundant and widespread kind of area with degraded soil and a depleted flora is heather moorland. This, as seen in the last account, shows a particularly well marked stability, or resistance to change. Over large areas in north-east Scotland this represents a self-regenerating system from which it is difficult to break away without gross technological intervention. The succession to birch, with its associated changes, is seen as one way of directing change in desired ways.

However, despite an extensive literature search, the only quantified evidence about the effects of birch appears to come from a small study over 20 years ago on the north Yorkshire moors by G. W. Dimbleby. This suggested that following colonisation by birch of a heather moor, the soil changed from a podsol to a brown forest soil, the humus from mor to mull, and the heather dominated vegetation to a herbaceous sward.

In 1973 we began a project to study the effects of birch. The approach is twofold: first, we are examining changes associated with different degrees of successional change at sites where birch has been invading heather moor; secondly, in experimenting along these sequences. So far, seven sites with suitable successional sequences have been found, situated from Perthshire to Sutherland.

The project is in effect an examination of the processes associated with a particular autogenic succession. The questions being asked are:

(i) What are the trends of any general effects associated with birch development?

(ii) What are the limits and rates of these effects with varying soil parent materials and climatic conditions?

(iii) What are the proximate and certain of the ultimate causes of the effects on soil and vegetation?

(iv) What are the implications of these changes for the development of a woodland flora?

(*J. Miles, T. Parish*)

4. SEED PRODUCTION OF *Betula pubescens*

Birch has been described as a prolific seed producer, with seed fall occurring between July and September. However, few data are available. The aim of this study was to examine variation in the annual seed fall in one stand of *B. pubescens* at an elevation of 38 m on Inverpolly National Nature Reserve, and typical of many in north-west Scotland. The Reserve managers were concerned at the continued decline of the wood and poor seed production was thought to be one possible cause of the inadequate regeneration. Circular seed traps were laid out at random in ungrazed birchwood and emptied at four weekly intervals from June to December and twice in the period January to May. When a monthly collection was not possible, the accumulated seed was included in the figures for the following month.

TABLE 1. Seed fall of birch (*a*) as a cumulative monthly percentage of annual seed fall; (*b*) annual seed fall (no/m²)

(*a*) *Season*	*1967–68*	*1968–69*	*1969–70*	*1970–71*	*1971–72*	*1972–73*
June	—	—	0·7	1·0	1·9	—
July	—	4·2	—	3·8	8·5	—
August	11·3	11·0	13·3	13·1	20·2	—
September	33·1	21·4	40·5	49·4	—	37·3
October	51·9	42·0	85·1	89·2	49·3	46·6
November	84·4	83·2	—	97·7	—	—
December	97·1	98·6	97·6	99·5	—	100·0
January–May	100·0	100·0	100·0	100·0	100·0	100·0
(*b*)	4,228	35,526	43,321	27,655	21,134	14,208

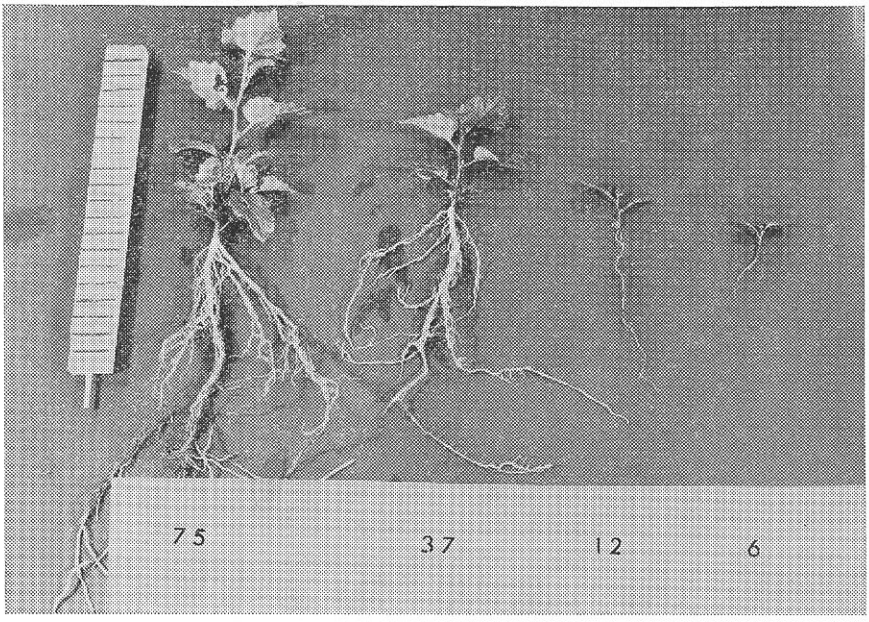
Seed fall was greatest in October–November, and was all but complete before the end of December (Table 1). The annual seed fall for six years ranged from 4,228 seed/m² to 43,321/m², equivalent to 7·5 to about 80 kg per hectare. While even the minimum seed fall may seem high, germination of birch seed from this area has only rarely exceeded 10 per cent. under laboratory conditions. Even so, the amount of viable seed produced is adequate for the regeneration of these woods, over a period of time. Observations suggest that this holds true for most birchwoods in the Highlands.

(*J. W. Kinnaird*)

5. GROWTH OF BIRCH IN SHADE

Established seedlings are rare in many plant communities with closed canopies. Under many birch stands, seedlings of the dominant aged up to 1 year are common, but few survive. This has been attributed to the effects of shade. However, partly because of the ubiquitous presence of grazing, particularly on the well developed swards under more open stands, evidence that the natural opening of the canopy as the stand ages enables regeneration to occur is equivocal. As part of a study on the importance of shade, the response of birch seedlings has been examined experimentally.

Plants were grown from seed in several degrees of shade. Growth measured by four parameters was positively and significantly related to relative light intensity (RLI). Mortality of seedlings was high (>50 per cent.) at 6 per cent. RLI and moderate at 12 per cent. (RLI). In a field experiment using transplants, similar responses of growth to shade and patterns of mortality were found.



Seedlings of *Betula pendula* grown at 75 per cent., 37 per cent., 12 per cent. and 6 per cent. relative light intensity (scale marked in cm).

Seedlings grew slowly in deep shade and by autumn they were still very small. However, mortality could not be attributed directly to low light intensity. In a number of cases, the death of experimental plants was associated with fungal attack. The fall of litter and vegetation in autumn which creates conditions suitable for fungal pathogens at ground level, also physically overwhelms small birch seedlings. Birch seedlings growing in deep shade may also be less able to recover from injury, particularly where photosynthetic surfaces are lost.

Shade appears to predispose young birch seedlings to an early death and must therefore be considered as a factor determining the abundance of older birch seedlings in birchwoods.

(*J. W. Kinnaird, E. Kemp*)

6. Structure and Succession in Woodland Communities

Little is known of the history and structure of the natural and semi-natural woods of pine and birch in the Scottish Highlands. Moreover, the role of earlier influences on the evolution of 'natural' woodland are not well understood. The woods of Glen Feshie in the central Highlands are typical of many in the region; they are mature and regeneration is suppressed. Because some of the historical background was known and data are available on the nature of current pressures and the responses to them, these woods provided a useful opportunity for historical interpretation that could assist in the evaluation of other woodlands.

The ages of randomly selected pine and birch trees were determined by ring counts made on cores extracted from the boles at a height of 1·30 m. On five

mature birch trees stem analyses were also made. Some difficulty was encountered in the identification of rings of birch where these were narrow, but other techniques are being investigated to clarify ring structure.

Regeneration of the birch woods appears to have occurred over long periods. However, in most, the period of active regeneration was 20–30 years with a small proportion of trees older and a few younger. One wood was an exception, but here there is evidence that birch regenerated progressively across the wood over a period of time. Abundant stumps and other remains of pine over part of this wood suggest that birch succeeded a felled pine wood; few pines remain.

The pine woods are either even-aged or have two distinct age groups. The dates of origin of the younger elements in these stands coincide with, or immediately post-date, the period when pine was felled in the area. Trees in the older age groups represent younger unfelled remnants of the previous stand; as evinced by the ring structure of this period, some of these trees grew very slowly for the initial 50 years, probably in the shade of older trees, while others had grown freely from an early age. It seems that the old pine woods had many gaps, and that grazing pressure must have been low. In two pine woods, one on very steep ground, regeneration occurred over a period of 150 years, terminating about 1860.

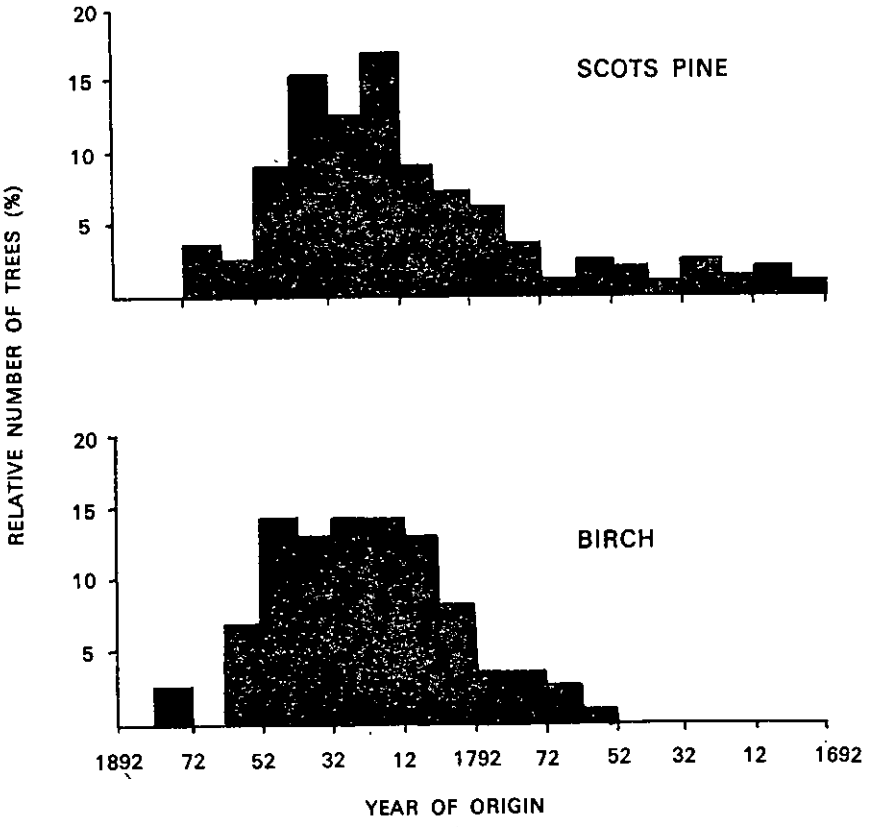


FIG. 1—Distribution of trees in Glen Feshie by estimated year of origin.

The histogram of the estimated dates of origin of trees in Glen Feshie (Fig. 1) illustrates the dominance of trees dating from about 1790–1860, with an abrupt cessation of regeneration at the end of the period. Natural mortality of older trees could account for the low numbers of birch pre-dating 1790. In contrast there is a continuity of small numbers of pine dating back to the latter part of the 17th century.

Considerable felling of Scots pine is recorded from this area in the late 18th and early 19th centuries, which would account for the sudden increase in regeneration. During this period when grazing by black cattle and sheep occurred, young birch reached a height of 1·30 m only after 20 years or more. Red deer, present in low numbers at the end of the 18th century, had become comparatively abundant by 1850 and little regeneration has occurred since then.

The influence of mans' activities, direct and indirect, is apparent in the location, structure, species content and extent of the present 'natural' woodlands in Glen Feshie. The potential of the woodland to regenerate is still considerable; seedlings occur widely though suppressed by grazing.

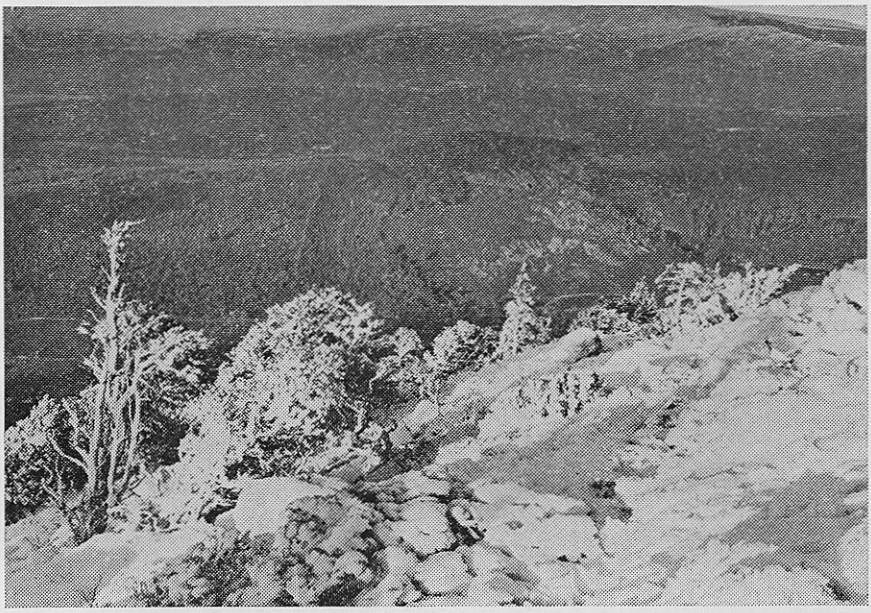
(J. W. Kinnaird, C. O. Badenoch)

7. Ecological Status of Montane Scrub Vegetation

One of the most notable features of Scottish mountain vegetation is the almost total absence of scrub at the upper limit of tree growth. In the eastern Highlands, tree-lines are usually depressed and are characterised by an abrupt change from woodland to dwarf shrub heath. Some fragments of montane scrub do occur, but usually these measure only a few square metres and are confined to cliff ledges inaccessible to animals and to fire. Presumably scrub cover was formerly extensive and was destroyed by fire. The reasons for its failure to regenerate are a matter for speculation, but there is evidence (p. 33) that grazing might be less prevalent than it is below the tree-line. A better understanding of the causes of the degeneration and extinction of montane scrub would provide a basis for management aimed at rehabilitation.

The best-known Scottish example of a relatively undisturbed tree-line is the upper margin of the pine forest on Creag Fhiaclach, Inverness-shire. Here, from 550 to 650 m, dense pine forest gives way to increasingly scattered and stunted trees and finally grades into juniper scrub. Above about 650 m there is heath, with a scattering of dwarfed pine and juniper saplings. In co-operation with Dr R. T. Ogilvie of the University of Alberta, work began on the description and analysis of this climatically determined tree-line in summer 1973. The aims were to (*a*) provide a basis for the conservation of a unique site, and (*b*) obtain data on the performance of pine and juniper at their altitudinal limit.

Sampling was by a series of belt transects and information was recorded on the distribution, density, age, size, vigour and distortion of both saplings and mature plants in relation to altitude and exposure. In addition, seed production and viability will be assessed. Field work is incomplete and results so far obtained have not yet been fully analysed. Some preliminary data on plant distribution and seed production are given in (Table 2).



Stunted pines encrusted with snow at 590 m on Creag Fhiaclach, 300 m above a commercial forest.

TABLE 2. Density (no./ha) of trees and shrubs, and seed production by pine and juniper, in different altitudinal zones on Creag Fhiaclach

Zone	*Cleared forest*	*Pine forest*	*Pine/juniper scrub*	*Juniper scrub*	*Montane heath*
Altitude (m)	300–410	410–530	530–590	590–670	670–750
Pine	133	147	229	43	28
Juniper	0	57	741	296	3
Rowan	6	7	29	23	0
Birch	439	154	8	13	0
Willow	0	3	4	6	0
Overall	578	368	1,011	381	31
% saplings	100	38	23	64	100
No. of pine seed/cone	25	24	20	16	—
No. of juniper seed/berry	2·2	—	1·8	1·1	—

There is a greater density of trees and shrubs in the pine/juniper scrub zone between 530 and 590 m than anywhere else on the study area. This is due mainly to an abundance of juniper (*Juniperus communis*) there. Saplings and checked plants are predominant, except in the pine forest and pine/juniper scrub areas. Both pine cones and juniper berries were plentiful in 1973, even at the upper edge of the montane scrub zone. However their seed contents were less at 600 m than at 300 m. Viability tests have yet to be done.

(*G. R. Miller, R. P. Cummins, S. M. Moyes*)

8. Regenerative Capacity of Mountain Vegetation

Rapidly increasing human activity on Scottish mountains during the past decade has highlighted the relative fragility of the vegetation there. It is easily damaged and, once destroyed, it recovers only slowly or not at all. Little is known about the stability of vegetation under extreme physical conditions and this deficiency is a serious obstacle to intelligent use.

In 1973, work began on processes involved in the recolonisation of bare ground at high altitude. Studies will concentrate first on the means and capacity of plants for regeneration since this is central to an understanding of successional changes. Accordingly, seed from ten plants with a wide altiduinal range was collected along a gradient from 300–900 m at five different study areas in the Cairngorm Mountains. The species comprised four dwarf shrubs, three graminoids and three herbs. In addition, seed was collected from six species normally confined to altitudes above 600 m. Samples were taken mostly from sites above 750 m, and up to 1,100 m. Germination tests will establish if there is any systematic variation in viability.

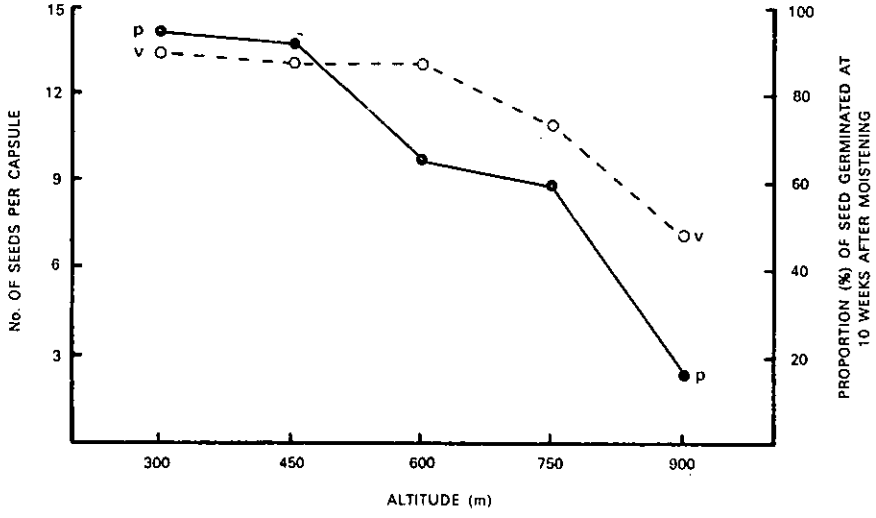


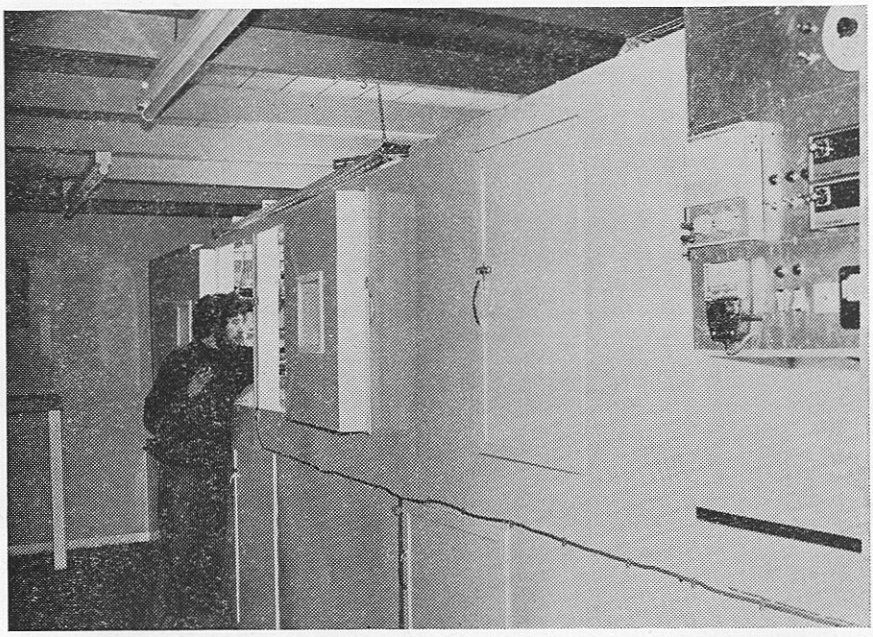
Fig. 2—Production (p) and viability (v) of seed of *Calluna vulgaris* in relation to altitude.

Only preliminary results for *Calluna vulgaris* are available so far (Fig. 2), but these show a substantial reduction in reproductive capacity with increasing altitude. Thus the number of seed declined from 14 per capsule at 300 m to 2 per capsule at 900 m; superimposed on this is a decrease in germination at six weeks from 86 per cent. to 41 per cent.

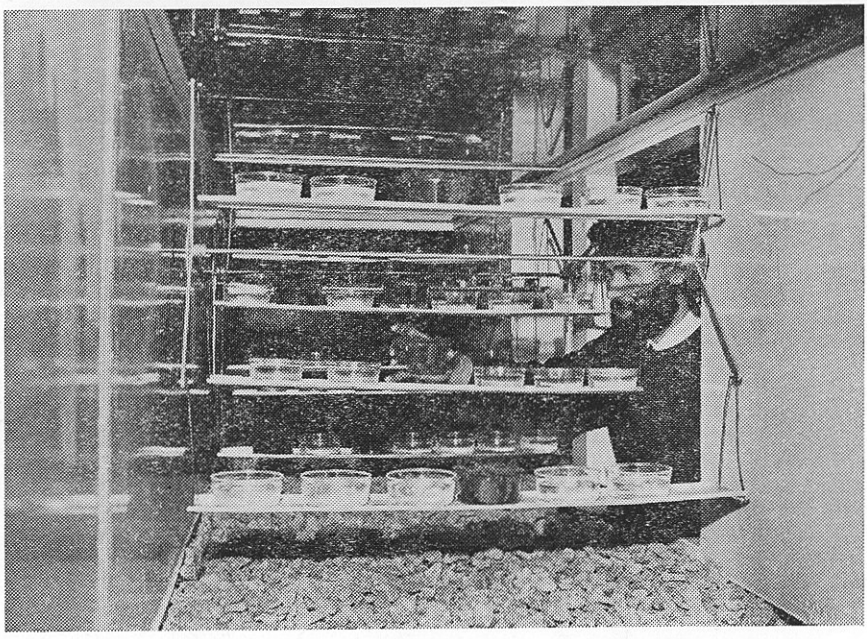
(G. R. Miller, R. P. Cummins)

9. Growth Chamber for Montane Studies

In order to perform laboratory experiments under simulated mountain conditions, a controlled environment growth chamber has been designed and its construction was completed at the end of 1973. The chamber can provide a wide range of wind speeds as well as being capable of working at sub-zero temperatures. Light intensity and humidity are also controllable, and a sytsem



The controlled environment growth chamber (above) and the system of movable trays (below)



of moving trays within the growth area gives the chamber a larger capacity than is usual with this type of facility. It is intended to use the chamber initially to study processes of colonisation and establishment of mountain plants under varying conditions of exposure.

(N. G. Bayfield, S. M. Moyes)

10. Modelling of Grazing Systems

Upland systems grazed by deer and sheep, although structurally simple have a temporal and spatial complexity of a high order. Modelling can assist the research and development process first by forcing implicit models into an explicit, testable form amenable to scientific method, and secondly by allowing managers the luxury of testing management procedures on a computer before they are implemented in the field. This has considerable heuristic value. The Range Ecology Group has therefore begun to develop a modelling strategy for upland ecosystems in conjunction with the Systems section of Merlewood Research Station.

Modelling upland grazing systems has all the problems of modelling other ecosystems together with some unique to these systems. Many of the inter-relationships are imperfectly understood and require much more research. This means that aggregated, often arbitrary, models are constructed. Spatial and temporal variation is an integral part of these subclimax systems, not just an unfortunate statistical feature. The history of the system is frequently its most dominant attribute and the state and development of the ecosystem at present can only be understood in this context. Despite this, a practical strategy is being implemented with some successes. In particular much of the development work has been done on St Kilda in the Outer Hebrides where the grazing system is dominated by Soay sheep. This has many useful qualities for a pilot trial of this sort. The general strategy is summarised in Fig. 3.

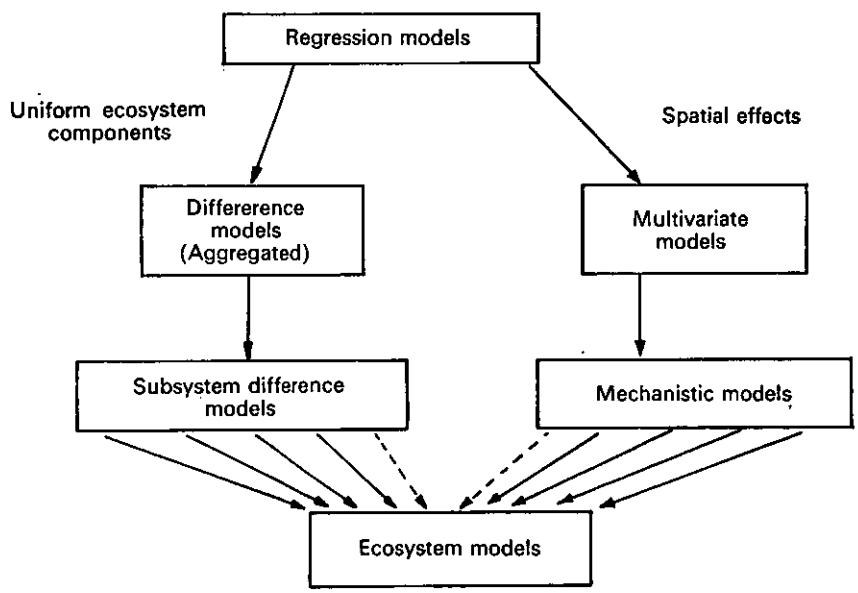


Fig. 3—Grazing system modelling strategy.

The basic strategy is to first use regression models to determine the driving variables of the system using aggregated components such as the sheep population as a whole. The second level is to separate the spatial effects from the models, treating animals and vegetation as uniform ecosystem components. Spatial features of the system are explored using discriminant and other multivariate models whilst the ecosystem component models are implemented as difference equation mechanistic models. At the third level, the spatial features of the system are explored using mechanistic models with the ecosystem component models disaggregated. Considerable effort is made to ensure transferability between the two modelling streams. The models used up to this stage are written in the BASIC computer language for implementation on the small interactive computer at Merlewood.

The final stage is to combine the spatial and uniform models into a realistic ecosystem model. This will require a larger computer and considerable computing time despite the parsimony of the multivariate approaches. This aspect of the strategy is currently moving towards a practical implementation. The level 1 and 2 models are at present being prepared for publication or are already published. The level 3 models are in the final stages of development prior to publication. The final stages of the strategy are the extension and generalisation of the models to systems grazed by domestic sheep and red deer.

(*C. Milner*)

11. The Impact of Grazing on the Uplands

Upland areas in Britain that have not been planted with trees nearly all experience grazing by larger herbivores of some sort. This grazing has frequently been condemned for inducing nutrient loss, decline in species richness and creating large areas of vegetation unsuited for secondary production. But it is not easy to show that these trends, if occurring, are caused by grazing, because their progress is often slow and obscured by the annual cycle of plant growth, so that significant changes can only be demonstrated after several years, during which continuous monitoring of grazing is required. So the evidence against grazing has been largely anecdotal, or associative, ignoring the other influences acting on, and the natural progressions occurring within, upland ecosystems.

In the last twenty years work by the Research Branch of the Nature Conservancy and other bodies such as the Hill Farming Research Organisation has begun to resolve the complexities of the inter-relationship between herbivore and range. In brief it has been shown that animal densities vary greatly within the units of management; this is due mainly to selection for vegetation types offering palatable food, but desire for shelter, social interactions and effects of disturbance are other causes. It is also established that even very low animal densities can have major impact by preventing tree regeneration, as young trees are highly favoured food. Vegetation is affected by herbivores in three main ways, firstly the differential response of the species present to being grazed, trampled and subjected to dung and urine, secondly the introduction of species from surrounding areas by passage through the animal or direct colonisation of the niches created by dung and trampling, and thirdly by modification of the cycle of decomposition with return of nutrients in more available but more concentrated form. The

relative importance of these processes varies with grazing animal and vegetation type, but all forms of impact increase in proportion to the numbers of animals present. As a result there are changes in the primary production and floristic richness of the vegetation being grazed, which culminate in change in vegetation type when critical grazing pressures occur for sufficient time.

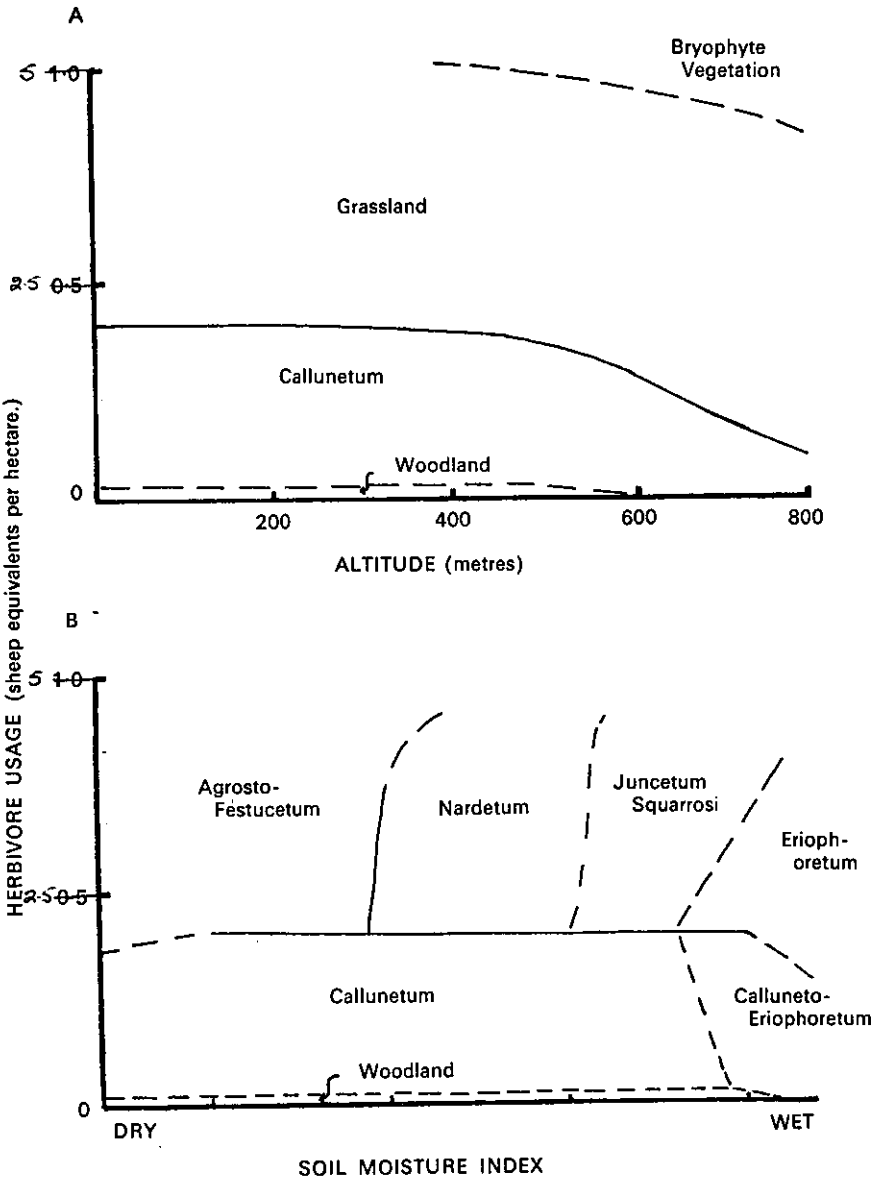


FIG. 4—The broad inter-relationships of main vegetation types on moderately well-drained soils (A) and at lower altitudes (B), with regard to grazing. Successions are not implied between all situations, and when occurring may be indirect.

Elimination of trees by grazing usually leads to the development of a dwarf-shrub heath. The main dominant is *Calluna vulgaris* except at high altitudes above about 750 m or on wet peaty soils. My present studies have aimed at quantifying the impact of grazing on these heather moors, and determining the thresholds for change to a range of grassy vegetation types, Agrosto-Festucetum, Nardetum, Molinietum and Juncetum squarrosi, associated with heavier grazing. This work has progressed for over four years, and the data obtained, combined with some from other studies, allow the inter-relations of these plant communities to be presented diagrammatically (Fig. 4) in terms of grazing densities and site attributes. These statements are highly simplified, and will be modified by variations in species of herbivore, season of grazing, age of *Calluna* when first subjected to substantial grazing and the extent to which the herbivore can select what it eats from the total range of food available, whilst sometimes other factors such as burning and snow-lie will be paramount to grazing in determining the occurrence of a particular vegetation type.

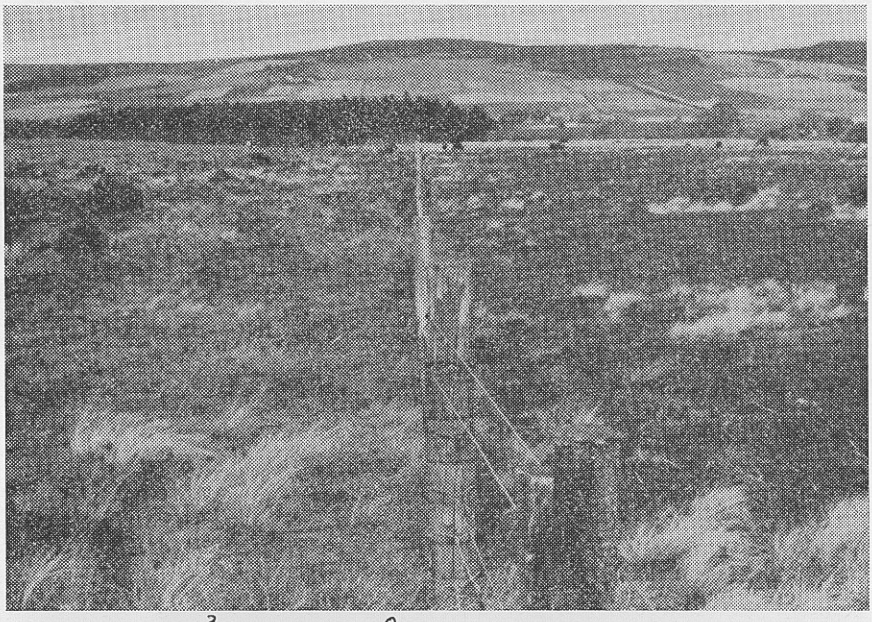
The effects of different animal species depend on their grazing habits, weight, and dung type. At one extreme, grazing by mountain hares (*Lepus timidus*) influences callunetum mainly by removal of *Calluna* shoot tips, inducing much branching, and when impact begins soon after a fire very dwarfed stands of heather develop (Welch & Kemp 1973). Ruminants graze the heather less selectively, and can sufficiently depress its growth to allow less competitive species to spread. Trampling contributes to overall impact in proportion to its frequency, concentration and the pressure exerted. With cattle, the dung pats form niches which permit substantial establishment by rapid-growing plants with good propagule dispersion, hastening the development of graminaceous and herbaceous vegetation. The dung of deer and sheep seems a less effective agent of change probably because the niche provided is generally smaller and subject to movement on disturbance.

My observations confirm that sheep cause change from Callunetum to grassland types, but cattle, under the conditions of the study, produced the sharpest decline of *Calluna*. For example, at the site in the plates following, *Calluna* cover fell from 40 per cent. to around 10 per cent. over three years with cattle densities approximately 1/ha. The Callunetum on the other side of the fence gives an indication of the grazing rate that maintains equilibrium; it has been unburnt for many years but kept short by sheep grazing. During the study period *Calluna* remained virtually constant, with perhaps slight increase in *Festuca ovina* and *Nardus* under an animal density averaging around 3 sheep per ha. Differences in effect between equal biomasses of deer and sheep appear small. However, sheep and cattle both prefer to graze Agrosto-Festucetum, so tending to maintain or extend this type of vegetation but having correspondingly less influence on the remainder. Red deer tend to prefer grassy Callunetum, and exert pressure more evenly over their whole range, so stands of grassy Callunetum take the place of both pure Callunetum and pure Agrosto-Festucetum.

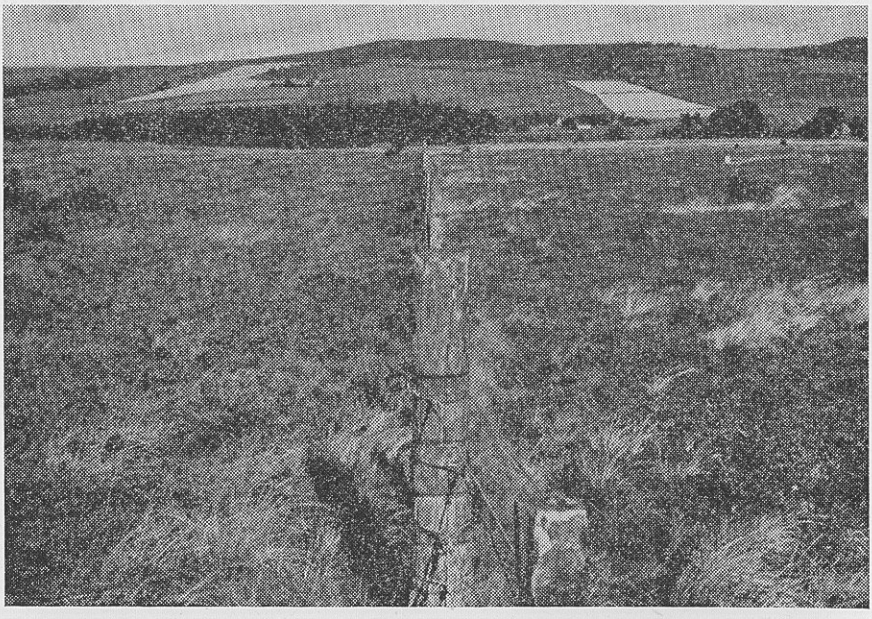
It is interesting that gorse increased perceptibly even under heavy cattle grazing as in the plates following. Gorse or broom occur in small amounts at many of the sites below 400 m, and spread in every instance (see also p. 32). It would seem that these shrubs cannot be controlled by present practices of grazing and burning, once their propagules reach ground in quantity, and

thus they could increase considerably in rough grazings at lower levels.

The main species that replace *Calluna* on wetter ground have overlapping ranges, and perhaps sward composition is determined by which is the first to colonise. *Molinia*, omitted for simplicity from Fig. 4, can grow in very wet sites but extends like *Juncus squarrosus* well into the range of *Nardus* on rather



Change between 1973 (above) and 1978 (below) in Callunetum subjected to heavy cattle grazing (to left of fence) and moderate sheep grazing (to right), on a peaty podsol soil.



drier soils. There is some evidence that cattle grazing gives *Molinia* a relative advantage, for at a wet site on lower Deeside where *Calluna* is being ousted, *Molinia* increased from 20 to 37 per cent. over three years, whilst *Nardus* increased only from 9 to 16 per cent. and *Juncus squarrosus* from 8 to 10 per cent. However, much more work is required before the inter-relationships of these important species are fully understood.

(*D. Welch, E. Kemp*)

12. Effects of Grazing and Burning on Soils and Vegetation

Various effects on upland range have been attributed to grazing and burning. Grazing changes vegetation in certain ways and under some conditions the long term effects can lead to soil instability and erosion. Burning, which is often associated with grazing on upland range, can have similar consequences. It can aggravate the effects of grazing or by itself create conditions of gross site instability. Changes of this order are clearly undesirable as judged by any standard. However, many changes that result from these two influences cannot be so readily evaluated. Indeed, few studies have been done to determine precisely what is the role of these factors under the various conditions of upland range, or how their effects vary with the frequency and intensity with which they occur. Certain aspects of this problem have been studied co-operatively with the Hill Farming Research Organisation.

The maintenance of soil fertility depends in part upon the re-circulation of nutrients either through decomposition of ungrazed herbage or through decomposition of the excreta of grazing animals. It has been shown (see Floate, *H.F.R.O. Report*, 1970) that the conversion of an increased proportion of the plant production to excreta leads to the liberation of increased amounts of 'potentially available' nutrients. It is impracticable to investigate experimentally the long term effects of different levels of utilisation on vegetational and soil characteristics. As part of this programme therefore evidence that would provide an indication of the effects of different management regimes over a long period was sought.

Vegetational contrasts often occur on the two sides of long established fencelines or walls in hill country. Twelve sites that could confidently be regarded as having been similar on the two sides of such dividing lines at some former time were selected for detailed study. Differences in the vegetation and soil morphology of paired sites along these fencelines have been investigated and the results are now being written up. Evidence has been found of the ameliorating effect on soil conditions of management regimes based on relatively heavy grazing that have produced sward-type grassland, compared with regimes that have maintained heather communities involving repeated burning.

(*I. A. Nicholson*, [*M. S. Floate*,] *I. S. Paterson*)

13. Liability of Saplings to Grazing on Red Deer Range

About 60 per cent. of the land surface of Scotland is categorised as rough grazing—extensive tracts with vegetation less than 1 m tall and populated by free-ranging sheep, cattle and red deer. Most of these 4·5 million hectares lie within the so-called climax forest zone. Yet centuries of felling and burning

have left only a few isolated patches of natural forest, and even the remaining pockets are in danger of further depletion because of their failure to regenerate. A complete loss of natural woodland is clearly not acceptable in terms of wildlife conservation.

The sparsity of natural regeneration is variously attributed to grazing, to a scarcity of viable seed, to unsuitable seed beds, and to rotational burning. All these factors play a part but, in most cases, the destruction or checking of seedlings and young saplings by herbivores is pre-eminent. For example, the lower ground in Glen Feshie constitutes the wintering area of a large stock of red deer. Here, where pine and birch are the forest-forming trees and are associated particularly with rowan and juniper, a recent survey revealed large populations of saplings below an altitude of 550 m: there were 186 birch, 58 juniper and 14 rowan per hectare. However, nearly 90 per cent. had been browsed, all were less than 50 cm tall. No pine saplings at all were found. Earlier studies of naturally occurring saplings of birch and juniper in Glen Feshie (1968–70 Report, pp. 33–35) indicated that although these were grazed at different seasons few individuals escaped damage over the year as a whole. Subsequently, seedlings of pine, birch, broom and gorse were planted experimentally at a wide variety of sites on the lower slopes and bottom of the glen. Comparisons were made of the rate at which plants were grazed so as to identify the circumstances in which regeneration would most likely develop if the deer stock were reduced. Periodic checks showed that liability to grazing did not vary much between sites but was closely related to the height of a seedling in relation to the height of the surrounding vegetation. Almost all tall and conspicuous plants were damaged by grazing within a few months. In 1973, four years after planting, only 23 per cent. of the original 150 seedlings remained alive. Gorse and broom had survived best and, indeed, all gorse plants had increased in height and spread since planting. Thus, if gorse escapes death during the period of early establishment and growth, it seems capable of a nett increase in bulk despite the presence of large numbers of deer (see also p. 29).

Observations of natural and planted saplings below 500 m in Glen Feshie indicated that trees and shrubs will not regenerate without fencing because red deer concentrate there in winter. However, deer are less active on higher ground. In winter, the upper slopes are snow-covered for much of the time and deer remain in the sheltered glen bottom; in summer, the animals are spread over a vast area ranging from 300 to 1,200 m. Thus overall grazing pressure is presumably less above about 500 m than elsewhere, and it might be reasonable to suppose that the liability of saplings to browsing decreases with increasing altitude.

To test this possibility, evergreen and deciduous seedlings were planted along altitudinal gradients ranging from 410 to 920 m. Pine and birch were chosen as convenient test species, although they are not necessarily suitable for establishing at high altitude. The sites were visited monthly, weather permitting, and any plants that had been grazed were replaced.

Both species were grazed more often at low altitude (410–520 m) than at high altitude (630–920 m). Overall, the liability to grazing at high altitude was about half that at low altitude, and it was similar only for a short period in late summer (Fig. 5). Over the year, birch was grazed more than pine. Birch was strongly preferred when it was in leaf in May-September, whereas

the evergreen pine showed a much less obvious seasonal variation. Two years after planting, 36 per cent. of the pine and 14 per cent. of the birch that were still alive at high altitude were ungrazed; at low altitude none had escaped grazing.

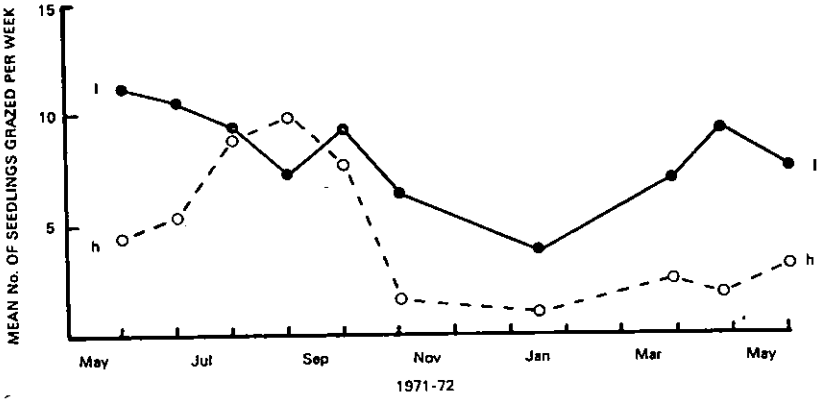


FIG. 5—Seasonal pattern of browsing on seedlings planted at low (l) and at high (h) altitude.

Pine and birch are both favoured browse species of red deer and heavy predation of saplings is to be expected. Earlier work (1968–70 Report, pp. 33–35) indicated that juniper, by contrast, was avoided for most of the year and was eaten mainly during periods of snow cover. Therefore juniper might be particularly suitable for establishing at high altitude because few deer are there when the plant is most liable to be grazed. Moreover, it occurs naturally up to 950 m and is presumably well-adapted to the montane environment, although it is nonetheless scarce there.

Juniper, pine, birch and rowan saplings were planted in autumn, winter, spring and summer 1972–73 and more planting was done in 1973–74. The work is as yet incomplete, but results obtained in 1972–73 show that rowan, as well as birch, is browsed mainly in spring and summer after the buds have burst. Similarly, juniper resembles pine in showing a much less marked seasonal pattern. At high altitude, all plants except rowan were less liable to grazing than those planted lower down (Table 3). This was particularly true of juniper.

TABLE 3. Liability of saplings to grazing at high and low altitudes.

	% grazed plants amongst 120 saplings of:				
Altitude	*Birch*	*Rowan*	*Pine*	*Juniper*	*Overall*
High (820 m)	23	46	44	15	32
Low (480 m)	46	49	97	69	65
Overall	35	47	71	42	49

Firm conclusions cannot be drawn from these data until the more extensive studies of 1973–74 are complete. Nevertheless there is a clear implication that factors other than grazing may be preventing the regeneration of juniper scrub at and above the potential tree-line.

(*G. R. Miller, R. P. Cummins*)

14. Deer Damage in Planted Woodland

In 1959–60 a programme of planting began at Beinn Eighe National Nature Reserve to create a more extensive tree coverage. All planted areas were fenced but the intention was eventually to allow red deer to enter the wood to graze and shelter. However, it is not known when or in what circumstances deer can be allowed into plantations without causing unacceptable damage.

In a management study, red deer were enclosed in plots of 6 ha and 8 ha in December, 1971. The 6 ha plot contained two large blocks of densely planted pine and a third area of mixed pine, birch, rowan and willow. The pines were 8–9 years old and 60–400 cm in height. The other plot was less densely planted. Apart from a few patches of bog myrtle and bracken, heather was predominant in the ground vegetation.

Three stags were placed in each plot for seven months. Damage was assessed by repeated observation of marked trees, by examining trees along line transects, and by photography. Trees were classified as small (>1¼ m), intermediate (1¼–2 m), and tall (>2 m).

Only 1 per cent. of the rowans were unbrowsed. Birch (85 per cent. damaged) was browsed less than rowan but almost twice as much as pine (43 per cent damaged). Overall, intermediate trees were browsed most and the tall trees least, but small pines were much less liable to browsing than tall or intermediate ones. Nearly all pines in low density areas and along the edges of blocks were damaged but the great majority of trees were within the blocks and less than half of these were browsed. On almost all damaged pines the lateral branches had been browsed, but the leading shoot had been removed from only 23 per cent. of them. Damage by thrashing and stripping was negligible.

There was little change in the general appearance of the plots at the end of the trial, partly because most browsed trees were small and therefore inconspicuous. If this trial had continued, few hardwoods would have developed to maturity. However, most of the pines, including those below 2m, would presumably have survived. It would appear that, where the density of deer in a plantation does not exceed the level of this trial, only minimal damage would result to dense stands of pines over 2 m tall. In return the deer might benefit from the shelter and browse provided.

(R. P. Cummins, G. R. Miller)

15. The Problem of Managing Range where *Molinia* is Dominant

Vegetation containing abundant *Molinia caerulea* (purple moor-grass) predominates in north-west Scotland, and *Molinia*-dominated grasslands are widespread and locally extensive. *Molinia*, a completely deciduous grass, thus forms a considerable part of the grazing available to sheep and red deer in this region during the growing season. It is customarily managed by burning to maintain a supply of readily accessible young shoots. Without burning, considerable amounts of litter quickly accumulate, masking the new growth in spring and creating a severe fire risk.

However, as shown in the last report, the increased attractiveness of *Molinia* after burning is short-lived. Also, and more seriously, burning favours *Molinia* and the equally deciduous deer-grass (*Trichophorum cespitosum*) at

the expense of heather (*Calluna vulgaris*), hence increasing the need to burn and also reducing the amount of winter forage. Certain types of *Molinia*-grassland can be converted to *Agrostis-Festuca* grasslands through intensive grazing, but the grazing utilisation of *Molinia*-rich blanket bog presents a considerable problem. It is very extensive in the north-west, and there is no evidence that it can be readily changed to a more desirable range type, or that stopping burning in itself causes a return to *Calluna* dominance. If the aim is production of sheep, red deer or other herbivores at present stocking rates, and if some sward improvement is not carried out, then burning is probably needed to keep the animals in reasonable condition. However, this will tend to increase further the dominance of *Molinia* and *Trichophorum* at the expense of *Calluna*, further reducing winter grazing and increasing the need to burn.

It was suggested in the last report that creating *Calluna*-dominant stands in places, and establishing scrub in others, would provide a greater diversity of forage and might thus be a partial answer to the problem. We are currently examining the feasibility of this on an area of *Calluna-Molinia-Trichophorum* dominated vegetation on a thin blanket peat at Beinn Eighe National Nature Reserve, Wester Ross.

We are attempting to establish bog myrtle (*Myrica gale*) from seed, and also two species of willow (*Salix aurita* and *S. cinerea*) by planting out rooted cuttings. We think that these may be able to grow on the peat and thus potentially constitute an alternative vegetation.

We are also attempting to kill the *Molinia* and *Trichophorum* and promote the regeneration of *Calluna* to try to create a stand where *Calluna* is dominant. About 0·4 ha was burnt in March 1972 in which 2×2 m plots in a randomised block experiment were sprayed in early summer with the selective herbicide dalapon (the sodium salt of 2, 2-dichloropropionic acid) to kill the monocotyledonous *Molinia* and *Trichophorum*. To encourage the regeneration we gave in 1973 the further treatments of sowing *Calluna* seed at a rate of 20,000 seeds per m^2, and a dressing of NPKMg fertilizer.

(*J. Miles, I. S. Paterson*)

16. Range Monitoring on Rhum

In 1971, twenty-one Highland cattle were introduced into Harris Glen, Isle of Rhum National Nature Reserve. The Range Ecology Group was required to monitor any subsequent changes in the vegetation.

The cattle had unrestricted access to other parts of the island and there was no certainty that they could be restricted to Harris Glen. Studies on the vegetation were therefore postponed until it was clear that the cattle would settle there. They did so after some initial difficulties. Observations showed that the cattle grazed mainly on the grasslands at the bottom of the glen, a small part only of the 1,600–2,000 ha in the vicinity. However, as the managers' intention was to expand the herd in future years, it was thought that the outlying range might gradually be used more heavily. Accordingly, it was decided to concentrate on describing the well used areas in 1972, and the remainder in 1973.

The main difficulty was how to monitor vegetation changes over such a large area with the limited time available. It was decided to select subjectively a limited number of small areas and to describe these intensively as a first

datum from which to evaluate future change. Most areas were chosen because change was thought likely with increased grazing pressure, but some were selected where change is unlikely to occur.

(J. Miles, I. S. Paterson, R. P. Cummins, G. R. Miller, A. M. Miles, E. Kemp)

17. Studies of Red Deer Performance and Condition

Studies of performance (growth, reproduction and survival) and condition (the state of animals at given points in time) are directly relevant to an understanding of population dynamics and productivity in wild red deer. Earlier work on the determination of age in red deer during the 1960's made it possible to study the processes of growth, breeding and survival using samples of shot deer. Two recent complementary projects gave a great deal of information on the growth and reproductive processes in wild deer living typically at high population densities in Rhum and Glen Feshie. Some data were given in the last report. Since then the field research has been completed and other aspects of the studies are being finalised in preparation for publication. No new data are presented in this account, though some of the salient features of the programme are reviewed.

A project on the annual cycles of condition and body composition in selected classes of red deer (on Rhum) gave relevant information on seasonal variations in growth and condition in relation to the changing resources available to the animals and the changing life cycle demands. Some preliminary results from this project were given in the previous report (1968–70, pp. 43–46). The study involved anatomical and other indicator methods of condition assessment and chemical determinations of gross body composition (water, fat, crude protein and minerals). It is not yet possible to relate the physical and chemical aspects of the study as the chemical analyses have not been completed. Nevertheless, the severe growth check shown by all classes of red deer from around November until late March points to the importance of nutritional inadequacies. In addition, the low reproductive success of sexually mature hinds is related to the slow recovery from the effects of pregnancy and lactation in this environment; the annual fat cycles in yeld and milk hinds show this very clearly. After the calving season (June), non-lactating mature hinds with no calf at foot (yeld hinds) show a rapid increase in fat reserves until late November, followed by a progressive decline until late March. However, lactating hinds with calves at foot (milk hinds) show no similar increase in fat reserves over the period after parturition until late autumn. Moreover, since ovulation seems to depend on condition, there is a tendency for yeld hinds to achieve a higher pregnancy rate (90 per cent. or more) than milk hinds (around 50 per cent.). Thus many hinds tend to breed a year and then miss a year. The high mortality rate found in red deer claves fits with the data on fat reserves; calves show almost no dissectable fat and a marked reduction in most carcase and organ weights over the winter. Although most of the soft tissues decline over this period, bones seem to continue growing slowly. This may suggest that minerals are less limiting than other nutrients during the first year of life.

Involvement with the management of red deer on Glen Feshie estate, as described in the previous report (1968–70, pp. 47–49), gave information on performance and condition in relation to sex and age, as by-products of

monitoring the population for management purposes. Data on age, carcase weight, condition, antler characteristics, and reproductive status were collected from 882 stags, 1,070 hinds, and 148 calves shot from autumn 1966 to autumn 1972.

Whereas the work on Rhum considered the characteristics of selected classes of deer throughout the year, the work at Glen Feshie gave information on all age classes of both sexes at one time of year. This was when the animals were in best condition. Hence, these two projects were directly complementary in the information obtained about performance.

Both projects showed that the first year of life is critical and hazardous. The studies also gave information on the performance of calves in relation to maternal factors. Special attempts were made to shoot the milk hinds and calves as pairs for this purpose. Using only those data from definite pairs, there are clear relationships between calf performance and hind performance. Such relationships would be expected as better hinds should nurture better calves, but the data indicate the quantitative effects of such maternal factors as age and condition.

(B. Mitchell, D. McCowan, T. Parish, I. A. Nicholson, J. M. Crisp, J. A. Stevenson, G. Sturton)

18. Nutritional and Physiological Studies on Captive Red Deer

The investigations described below were carried out at the Rowett Research Institute (1970–1972), and we gratefully acknowledge the help and facilities made available to us.

The small adult size, late attainment of puberty, and low reproductive rate of red deer in the Scottish uplands suggests that the nutritional status of the animals is low. In order to assess the extent to which wild deer are undernourished in such habitats, it is necessary to establish the potential of red deer of this genotype under optimum feeding conditions. It is difficult to measure the nutrient requirements and intakes of free-ranging deer. Our initial studies have therefore been carried out on captive animals, kept on known feeding regimes. Their growth and development can be used as yardsticks against which those of wild deer can be assessed.

Growing calves have the highest relative nutrient requirements, and are most vulnerable to deficiencies. Winter mortality of wild deer is highest in this group. Our studies have therefore concentrated on various aspects of growth in red deer calves.

Milk Yield and Composition

Milk samples from five hinds were analysed. During the first 3–30 days of lactation, the milk contained an average of 21·1 per cent. total solids (8·5 per cent. fat, 7·1 per cent. protein). Late lactation milk contained an average of 27·1 per cent. solids (13·1 per cent. fat, 8·6 per cent. protein).

Milk yields were measured by weighing calves before and after suckling, six times in 24 hours. In well-fed deer, peak yields of 1,400–2,000 g/day were recorded, but the yield from an underfed hind was much lower. Over the first 150 days of lactation, well-fed hinds produced 140–180 kg of milk, whereas an underfed hind produced only 65 kg. Well-fed hinds ate very large amounts during lactation, and gained weight after calving, losing it again later,

whereas the weight of the underfed hind fell and then rose again. The weight changes of lactating wild hinds and their calves might be useful to give an indication of the nutritional adequacy of the range in the summer and autumn.

Growth Rates of Suckled Calves

Five hinds were kept together with their calves (four pairs over a complete lactation), and the growth of the calves, and their milk intakes, were recorded. They were fed on good quality dried grass plus some concentrate. All but one were on free-feeding or high plane diets. The exception was one hind kept on a very restricted food intake.

Initial growth rates over the first month were 270–420 g/day in the calves suckled by the well-fed hinds, and 90 g/day in the calf of the underfed hind. The former weighed 22–32 kg at 60 days of age, and 35–57 kg at 120 days. The data were compared with those of wild calves shot on Rhum. Taking hind size and calf sex into account, the growth of Rhum calves appeared to be about as good as that of the well-fed calves up to 60–80 days of age (mid-August–September). After this, the captive calves continued to grow throughout the winter, whereas wild calves lost weight during the winter and in spring were much smaller than the captive ones. The data suggest that mid-summer nutrition may not limit milk production and calf growth, but that limitations set in from about September onwards.

Growth of Concentrate-Fed Deer

In 1970-71, an experiment was carried out to study the growth of red deer calves fed on a barley-based concentrate, after weaning at 7½ weeks, in order to assess their growth potential on a very nutritious diet. The 10 calves were split into two groups, on free-feeding and restricted food intakes respectively. The experiment was terminated at 48 kg live weight. A similar experiment was started in 1971, using two stags and three castrated stags (one stag died and was replaced) on free-feeding. One animal from each group was killed for carcase analysis at 48 kg. The second experiment was continued until the end of 1973.

Initial growth rates, up to 48 kg, were 320–350 g/day in males fed to appetite, and 190–270 g/day in females, in the first experiment. In the second experiment, started in 1971, initial growth rates were 180–250 g/day in the castrates and 230 g/day in the one stag to reach 48 kg. Feed conversion ratios (dry matter intake/liveweight gain) in 1970 compared very favourably with those for sheep on the same diet, but were lower in 1971. Continuation of the second experiment has demonstrated very marked seasonal changes in appetite, which were much more accentuated in the stags than in the castrates. Voluntary intakes were much lower in winter than in spring and summer.

Maintenance Requirements

From past records of red deer kept at the Rowett Research Institute since 1966, it has been possible to extract data on the food intakes of deer when their weights remained steady, and thus to estimate their maintenance needs. These are similar to the needs of other species of deer studied, and of cattle, per unit metabolic weight ($kg^{0.75}$), but are higher than the needs of sheep.

The nutritional studies so far carried out raise several points of ecological importance. Our studies on perinatal mortality have shown that this is quite high in captive stocks. Similar work might be carried out on wild stocks, as the extent of this mortality is one of the gaps in population dynamics studies. We have shown that the growth potential of red deer of Scottish origin is much greater than the actual growth of wild hill stocks, and that the differences set in from early autumn onwards. The nutrient intakes of wild hinds appear to be sufficient in mid-summer to support high rates of milk production, although this may be at the expense of some loss of condition in the hinds, since fertility in October is lower in 'milk' than in 'yeld' hinds. From autumn onwards, all hill deer are subjected to nutritional stress. Winter losses of condition are caused by a combination of low appetite, low digestibility and, at times, actual food shortages.

(*P. Arman*)

19. Studies of Red Deer Dispersion

Many deer management problems are associated with deer movements and distribution. The main factors affecting the movements and distribution of red deer are likely to be food, weather and interactions between animals of the same or different species.

It is widely recognised, though inadequately documented, that red deer stags and hinds segregate for most of the year and that the areas they occupy in winter are traditional and geographically separate. As this segregation of the sexes appeared to be a basic feature of red deer biology, we decided to study the factors affecting it as a first step towards understanding the processes involved in deer distribution. Glen Feshie was the study area, and the intention was first to describe the pattern of dispersion throughout the year, and then to investigate the possible mechanisms involved. Initially the work concentrated on spacing and social behaviour, and we have recently started to investigate the role of food and shelter. The final data for the spacing study are at present being analysed, but some preliminary observations are available.

Segregation and group size

Segregation of the sexes at Glen Feshie was not complete, and the winter ranges of stags and hinds overlapped. Each sex however, tended to concentrate in different areas, stags occupying a lower part of the valley system than hinds. Adult stags tended to associate less with hinds than younger stags, but the extent of segregation and group size was variable.

Within the sexes there was a tendency for animals of a similar type (e.g. age, condition) to group together, and within groups, animals of a 'like-kind' tended to associate; with stags, the younger animals were usually found at the edge of the group and, when on hillsides, usually above the older ones. Groups were not permanent and individuals joined or left frequently. However, there were apparently some cohesive units (e.g. family parties) within the larger groups. Stags moved less within their winter range than hinds, the latter moving up and down the glen according to weather conditions. When hinds moved away from their wintering areas in spring, stags moved into these places. In July and August, stags were found in the same general area as hinds, though occasionally on higher ground.

Process involved in segregation

Without experiments it is difficult to separate cause and effect. The evidence so far suggests that stags are dominant to hinds in direct encounters, and when groups were mixed together (either naturally or when disturbed) it was usually stag-dominated groups which joined other deer and hind-dominated ones that left. This, together with the evidence from the association of individuals of 'like-kind' within groups, suggests that social behaviour may be more important than differential habitat selection. However, studies on the differences in selection for food and shelter by stags and hinds are in progress.

Differences in food selection between stags and hinds

Stags and hinds may have different nutritional requirements so that they seek different kinds of forage. Alternatively, stags and hinds may eat different foods because they occupy different areas for other reasons. We need to know first whether the foods eaten are different, and second whether any differences result from selection or availability.

Other research projects gave opportunities for investigating some aspects of food selection by stags and hinds. The proportion of nitrogen in rumen contents has been used as an index of forage quality in research on wild ruminants, but little experimental work has been done to test the underlying assumptions of this technique. It is assumed, for example, that food quality is proportional to the protein content and that this in turn is proportional to the nitrogen content. It is further assumed that there is a direct relation between the nitrogen content of rumen material and the original food material. This last assumption was tested at the Rowett Research Institute during experiments using rumen-cannulated red deer. A high correlation was found ($r=0{\cdot}96$, $n=112$) between food nitrogen and rumen nitrogen. Rumen samples collected on Rhum from samples of deer shot at different times of year were analysed for nitrogen content. All classes of deer showed a distinct annual cycle of rumen-nitrogen. This probably reflected the annual cycle of forage quality. However, stags had a lower rumen-nitrogen content than hinds through most of the year, except in mid-summer. Thus hinds may get higher quality forage than stags through most of the year. Alternatively a physiological factors may explain this difference, and further work is required.

As a further check on this apparent difference between stags and hinds, rumen samples were collected from stags and hinds shot at Glen Feshie in autumn, winter and spring in 1972–73. Three special areas were chosen representing one area occupied only by stags, another area occupied only by hinds, and a third area regularly used by both sexes. Stags and hinds were shot separately in these three areas. The solid and liquid rumen fractions were collected separately for further work on the interpretation of rumen nitrogen. Chemical and botanical analyses on the material collected are in progress. However, the material from this study should provide information on whether there are differences (i) in plant selection by the sexes, (ii) in their ability to select food for quality or (iii) that there may be a possible physiological difference between the sexes that accounts for higher rumen nitrogen in hinds.

The role of shelter

From observations at Glen Feshie, it seemed that weather had a marked effect on the distribution of the deer, especially in winter. Also, because stags were invariably found on lower ground than hinds in winter, there could be differences in shelter between the areas occupied by stags and hinds. This possibility has been tested by simultaneous measurements of the microclimates experienced by groups of stags and hinds. This is a preliminary stage to later work on the interaction of food and shelter as factors affecting the distribution of red deer.

(*B. W. Staines, T. Parish, J. M. Crisp, J. A. Stevenson*)

20. Parturition and Maternal Behaviour in Red Deer

Parturition and associated behaviour were studied in six hinds kept indoors. Four gave birth normally. One had prolonged labour, with a posterior presentation and everted uterus. Another had a posterior presentation, the birth was assisted and the calf died of an umbilical haemorrhage into the uterus (a foster calf was accepted). In two of the six hinds, lactation started a day after calving. This high incidence of problems may have been due to the stress of captivity. However, earlier work on natural mortality in wild red deer in a number of different study areas showed a high incidence of mortality amongst calves during the calving season as well as in winter, the latter being the main period of natural mortality amongst older deer. Furthermore, some calving difficulties were noted almost every year during calf tagging operations in all of these study areas.

In June–July 1973, a study was carried out at the Hill Farming Research Organisation/Rowett Research Institute experimental deer farm at Glensaugh, using a team of observers. The deer were kept in large fenced paddocks and were usually unaware of being watched. Calving was observed in 27 hinds. From a total of 55 pregnant deer, 46 calves survived the perinatal period. None of the hinds died, but a few needed veterinary assistance. Calving difficulties were less frequent in these free-ranging deer than in the small sample of captive hinds studied earlier, but perinatal calf mortality was quite high.

(*P. Arman, J. M. Crisp, J. A. Stevenson*)

21. Management and Development of a Deer Forest

By agreement with the proprietors, the West Highland Woodlands, the 17,400 ha deer forest of Glen Feshie in the Cairngorm Mountains was made available in 1966 as a field research area. It was also agreed that the Nature Conservancy would be associated with the management and development of the estate, and that the effects of recommended changes in management should be documented. Thus, in addition to the use of Glen Feshie as a field centre for a variety of research projects, it was intended to use it for an *ad hoc* case history study (1968–1970 Report, pp. 47–49).

The principle management aims of the estate were (*a*) to take measures aimed at improving the 'quality' of the deer herd, (*b*) to increase the area of afforestation, and (*c*) to integrate afforestation with deer management, paying due regard to the interests of nature conservation. A number of recommendations were made with the objective of encouraging trends most

likely to meet the main requirement of improving the deer stock. It was recognised that a marked response in performance (growth and reproduction) was unlikely to occur without gross interference and heavy inputs. At the same time the existing poor performance of the deer population had to be considered in relation to the substantial area that it was intended to remove from the deer range as a result of fencing for woodland planting. The total area of planting envisaged was 1,000 ha, representing 16 per cent. of the winter range below 600 m. The recommendations were designed to meet what were regarded as the minimum requirements to make the exercise worth while as a case history study, but within the limits of inputs and interference that were acceptable to the estate.

The main recommendations agreed were (*a*) an increase in the hind cull to a level that theoretically would bring about a decrease of 25 per cent. over a number of years; (*b*) the appropriate siting of woodland blocks to take into account deer distribution and the quality of the range, as well as the ultimate sheltering value to be gained; and (*c*) improvement of the low lying pastures for use by deer especially in autumn after the rut and in the spring before the deer moved to higher ground.

In recommending the higher cull of hinds there was no certainty that the numbers could be reduced by this means as there was no control of incomers. However, this was an experimental element in the development recommendations to determine whether or not culling was an effective means of controlling numbers on one management unit that formed only a part of a much more extensive area of range.

A number of *ad hoc* studies have been done on Glen Feshie, both as an aid to preparing the management plans and for purposes of surveillance. A substantial part of the recommended management 'package' has been put into effect. However, while the level of culling has increased over the years it has not yet reached the critical level necessary to reduce numbers.

(*I. A. Nicholson, D. McCowan*)

22. Footpath Studies

Footpaths are the key to controlling the distribution of people in nature reserves and wilderness areas. Our research has been directed towards understanding the causes and effects of footpath deterioration. Studies in the Cairngorms have shown that the width of a path is closely related to the roughness and wetness of the path itself and of the surrounding terrain. These observations provide guidance for the maintenance and lay-out of footpaths.

The problems of analysing short paths of a few miles are quite different from those encountered on longer routes. A joint investigation with the Countryside Commission attempted to measure the use and condition of the whole of the 430 km Pennine Way (*Pennine Way Survey, Countryside Commission 1973*). This study was undertaken in order to obtain information on the condition and causes of deterioration of the footpath that would be useful to managers of ground through which it passed. The route passes through or close to several Sites of Special Scientific Interest and forms a transect along the entire length of the Pennines. Sampling the Way at approximately 50 m intervals required the design of rapid survey techniques. These were applied satisfactorily in the summer of 1971, and this was the

first time a long distance footpath had been analysed in detail. Data on the amounts of wear and levels of use indicated that most of the Way was in satisfactory condition, though some sections were in need of immediate maintenance and in a few cases, of substantial reconstruction. An increase in use of more than twenty-fold would be required to produce the wear found on the most heavily used sections, along the whole route. This study provides a baseline against which any future change in wear or use can be compared.

(*N. G. Bayfield, S. M. Moyes*)

A sample transect laid across the Pennine Way at Edale.

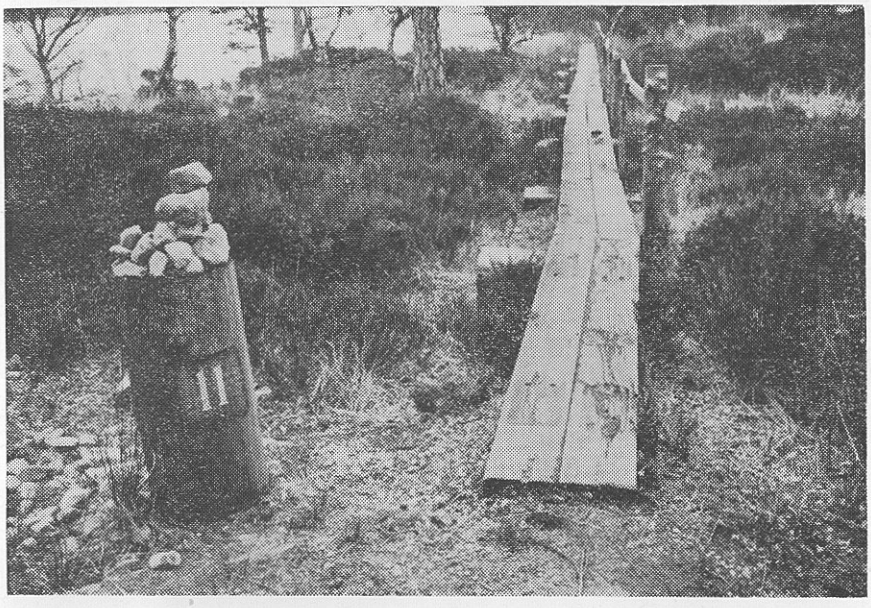
23. Techniques for Recording People Pressure

Studies of human impact require quantitative information not only on the result but also on the cause. The technology required was almost entirely lacking, so a range of counting devices and techniques were devised and tested. These included photo-electric counters (such as the 'Photoflux' counter) and counters for fitting to gates and stiles. The latter proved particularly useful for routine recording, and they are being widely used by Nature Conservancy Council and other bodies.

Interview surveys have been used on footpaths and nature trails at Stac Polly, Beinn Eighe National Nature Reserve, and in Speyside, Deeside and the Lake District. The first nature trails in this country date from about 1961. There are now more than five hundred, including many in nature reserves. However, so far there are virtually no measurements on levels of use by people, the types of persons involved, or the effects of different kinds of publicity or siting on demand for trails by visitors. Our surveys were designed to provide some basic statistics of a compatible nature, for trails in differing

ecological and geographical situations. It is hoped that these data will assist the rational planning of trails as well as being useful in the routine management of reserves for people.

(*N. G. Bayfield, S. M. Moyes*)



A device to count people automatically installed in a hinged section of a wooden path at Ben Eighe National Nature Reserve.

24. Damage and Restoration of Vegetation near Ski Lifts

Studies of the impact of skiing developments began in 1967 and only a few aspects were pursued after 1970. Much of the damage to the ski slopes was caused by machinery, such as tracked vehicles. These often completely stripped the vegetation and the ground was then liable to erosion, with debris being deposited downslope onto otherwise undisturbed vegetation. Erosion was at its greatest in 1969 but there has been a marked decline since then attributable to the reseeding of damaged ground, provision of drains and grading of dirt roads.

A series of experiments began in 1968 and 1969 to examine the effects of burial by erosion debris on the indigenous and reseeded vegetation above 750 m. The vegetation involved consisted mainly of short mountain heath species that were completely buried by quite shallow depths of erosion debris. Thus 7 cm was sufficient to cover all species in an *Empetrum-Rhacomitrium* heath at 1,000 m. The recovery of experimentally buried vegetation was followed from 1968 to 1971. The rate of recovery was found to depend on the proportion of the original cover completely buried. Recovery at best took several years, but on plots buried to 5 and 10 cm it was almost negligible (Fig. 6).

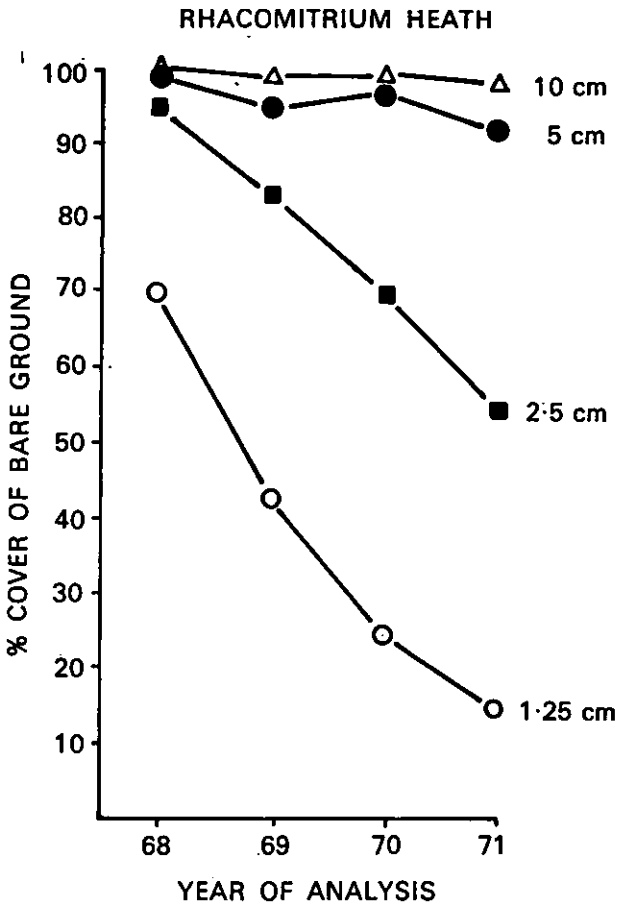


FIG. 6—Declines in the cover of bare ground through recovery growth of *Rhacomitrium* heath following burial by various depths of gravel.

On Cairngorm, reseeding of damaged ground with a mixture of commercial grass seed has been largely successful even up to 1,100 m. The sward is bright green, especially in the spring, and does not blend well with the natural vegetation of the mountain. In 1969, when most swards were only one or two years old, there was little or no colonisation by indigenous species, except below 750 m where numerous seedlings of *Calluna vulgaris* were present. However, bryophytes were conspicuous even in the season of sowing. A second analysis in 1972 revealed considerably more colonisation by a wide range of indigenous species. Although there was still less than 5 per cent. cover it is possible that the native vegetation may eventually supplant the grasses.

(N. G. Bayfield, S. M. Moyes)

25. MANAGEMENT OF RED DEER AND DEER-OCCUPIED LAND IN PARTS OF EUROPE AND NEW ZEALAND

The red deer is clearly a very successful and adaptable species, and its sporting, meat-producing and aesthetic values have been long recognised by man. Indeed, the present distribution of the species in the world is largely

explainable in these terms. The animal occurs naturally throughout the more temperate parts of the Old World from the sub-arctic to the Mediterranean climatic zones, and it has also been successfully introduced into such countries as Australia, New Zealand and Argentina. Throughout its range, it is hunted for sport as well as meat, and it is kept in deer parks largely for its aesthetic qualities. The earliest deer parks may, however, have more akin to meat reserves or deer farms. An interest in the farming of red deer which has developed over the past few years may have resulted from two recent factors. First, we have seen the development of systematic game cropping and of game ranching in Africa. Second, Germany has shown increasing interest in venison and other game products thus stimulating a lively export trade in red deer carcases from such countries as Britain, Poland, Hungary and New Zealand. Over the past few years, for example, Scotland has been exporting annually over 30,000 and New Zealand over 100,000 red deer carcases to West Germany.

Nevertheless, in most places, the prime management objective with free-ranging red deer is sport, with venison as by-product. On the Continent there are long traditions of trophy-oriented red deer husbandry whereas in Scotland there are equally long traditions associated with deer stalking as a sport. In Scotland the 2·8 million ha of deer occupied land comprises over 300 sporting estates managed largely to suit the needs of deer stalking.

On the other hand, wherever the red deer occurs, there are problems of impact on the habitat or of conflict with other land-use objectives. The red deer, a ruminant, is well able to survive at high population density on poor quality food resources. Therefore, without adequate population control, the red deer can seriously affect its habitat. Where red deer are maintained for secondary management purposes in areas of commercial forest, there is an obvious need to restrict damage to acceptable levels. Even in areas where red deer are the primary objectives of management the state of the habitat is also of prime importance.

The policies and practices of red deer management should be closely related to the management objectives. The size and age-sex composition of a deer population can be manipulated in different ways to suit different objectives. Producing trophy quality stags and producing meat are at opposite ends of the spectrum of management possibilities with regard to the size and composition of the population; the former requires an even sex-ratio with a long age distribution of stags whereas the latter requires an excess of hinds with just enough stags to mate them.

But the ways in which red deer are managed in different countries are influenced by hunting traditions, game and wildlife legislation, firearms controls, tourism and a variety of other factors.

The award of a Winston Churchill Travelling Fellowship in 1973 made it possible to gain first-hand experience of the various factors involved in managing red deer and deer-occupied land in selected parts of Europe and New Zealand. The objectives were to look at the various factors affecting management policies and practices, and at some of the research in progress. It was hoped that this experience would be relevant to the deer situation in Scotland, and to planning future research work.

The three month study tour comprised visits to Sweden, West Germany, Poland, Hungary and New Zealand. These countries were selected on the

basis of differences from Scotland in the status or management of red deer.

Sweden has a relict population of native red deer and attempts are being made to repopulate some of the former red deer range with native stock. However, the major big game animal in Sweden is the moose and at present almost 40,000 moose are being cropped annually. Although there are comparatively few wild reindeer in Sweden at present, there are large herds of domesticated reindeer which live a free-range existence for most of the year in Northern Sweden. Aspects of management and research with regard to these two important deer species in Sweden was relevant to the red deer work in progress in Scotland.

Germany, Poland and Hungary have long traditions of trophy-oriented red deer management as secondary objectives in the management of woodlands and commercial forests. Managing red deer for maximum individual quality, especially antler characteristics, involves a severe control of population density, careful selective shooting, and extensive winter feeding. The whole package of trophy-oriented management including hunting traditions, supporting legislation, and economic factors showed many interesting contrasts with the red deer management in Scotland. It would not be prudent in this report to isolate aspects of Continental management policy or practice which might be directly relevant to Scotland. It is interesting to note that there seems to be a progressive increase in the growth rate of red deer as one proceeds from north-west Europe towards the Carpathians; the biggest red deer are apparently found in Transylvania. It is difficult to judge on present evidence whether this represents a genetic cline or whether environmental conditions are responsible. It is widely assumed that red deer in south-east Europe have a higher growth potential than those in north-west Europe, but there seems to be little evidence based on captive animals reared under controlled conditions. Nevertheless, the hunting museums in Hungary show many red deer trophies (from the flood plains of the Danube, and from the Carpathian mountains) weighing 12 kg or more; an average mature Scottish stag has antlers weighing about 2 kg. However, compared with the heavily stocked, poor quality, exposed hill-land on which red deer live in Scotland, these areas of eastern Europe could be expected to produce better growth rates in red deer. The flood plains of the Danube have a low population density of red deer as well as a more favourable climate, richer soil and more luxuriant vegetation. Similarly, the natural forests of the Carpathians with the large predators (wolves and lynx) which still occur there must also be more favourable to high growth rates in red deer.

In most parts of the Continent where the deer are managed in commercial forests, winter feeding is a major item of management. Apart from the collection and storage of natural materials like acorns and horse-chestnuts for winter feeding, the deer are also given hay and sileage. In addition, in many forests special crops are planted and deer meadows are created. These open areas are also used for siting high seats for the control and selective shooting of the deer.

The high income from trophy individuals is used to offset some of the costs of deer damage to forestry and agriculture as well as other management costs such as winter feeding.

Throughout the Continent, aspiring hunters have to pass special examinations before they can obtain a licence to hunt or shoot. This kind of

apprenticeship in hunting laws, traditions and wildlife biology, made an interesting study in itself.

The present status and history of the red deer in New Zealand have been well documented in the New Zealand forestry and wildlife literature. However, it was useful to gain first hand experience of deer habitats and deer management by visiting areas and meeting people concerned in different aspects of the deer situation. The early European settlers in New Zealand found themselves in a virtually mammal-free environment. Acclimatisation societies were formed over a century ago with a view to filling the environment with potentially useful (meat and fur producers) and attractive animals from many parts of the world. Red deer were spectacularly successful in this favourable—predator, parasite and disease-free—luxuriant environment. As part of the acclimatisation policy, introduced deer were given absolute protection from hunting until the 1920's when serious habitat-impact problems came to be recognised. Destruction of native forests ('bush') in large, steep-sided catchment areas with soft rocks and high rainfall, produced serious problems of soil erosion and increased risks of flooding. Much of the best agricultural land and most of the settlements were on the flat valley bottoms where increased flood risks were serious matters of concern. From the 1920's onwards attempts were made to control the deer by government hunters with bounty incentives. On account of the terrain it was difficult to concentrate efforts on those areas most vulnerable to deer damage. Thus during the 1950's deer and some other introduced mammals were officially declared 'noxious' and the policy was to exterminate them. Even large scale poisoning campaigns using carrots treated with the poison '1080', often scattered from aircraft, had comparatively little effect and at high cost.

However, the development of a venison export trade to Germany stimulated meat hunting both on foot and using helicopters, and this started to reduce the deer. Use of helicopters meant that previously inaccessible areas (the alpine grasslands and the more remote valleys) could be exploited by the hunters. The meat trade also stimulated an interest in deer farming in New Zealand and also trade in other red deer products. Some by-products of red deer (antlers in velvet, tails, tendons and penises) are highly valued as aphrodisiacs in the Far East, and these items are also exported from New Zealand.

Special interest was taken in the work of many research institutes in Europe and New Zealand investigating ecological aspects relevant to the management of deer and their habitat. Much of this work centred around food preferences and impact at the fundamental level but also on applied *ad hoc* problems of reducing deer damage. Damage control is being investigated in three different ways: by the control of animal numbers, by using extra winter feed or specially planted crops to divert deer from vulnerable plants, and by the use of repellants or protectants. Assessment of deer numbers, in contrast to the Scottish Highlands, is a particularly difficult problem in woodland habitats and various techniques are being tested in woodland habitats. Some of these techniques, like the use of pellet counts, simply give a comparative index of deer numbers whereas others like the 'drive-census' technique attempt to count all the deer in sample areas of forest. Some of the techniques and lines of research are of direct interest to both the deer situation in Scotland and to the planning of new research.

(Brian Mitchell)

Wetlands Research Group

P. S. Maitland

1. Introduction

This research group in the Institute of Terrestrial Ecology is responsible for a wide range of work on natural wetlands habitats. It consists of two sections. One deals with fresh waters, which cover the full range of open water habitats from large lakes and rivers to small pools and springs, and the other with peatlands which include all peat-forming systems such as the valley-mires, raised-mires and fens of the lowlands and the extensive blanket-mires of the uplands. Because of basic ignorance of the wetland environment, much of the work so far carried out by the Group has been descriptive. It has also been biased towards the needs of conservation management.

Research begun in 1968–70 and described in the last report has continued. Some new projects have started. The Loch Leven IBP Research Project developed under the co-ordination of the Wetlands Research Group, and the combined study involved the Freshwater Fisheries Laboratory, Pitlochry, the Wildfowl Trust, and the staff from various departments in the Universities of Aberdeen, Dundee, Edinburgh, Newcastle, St Andrews, and Stirling. Most field work for this project was completed in 1971, and much of the effort since then spent on processing data and writing-up. Many members of the Group attended an international meeting at Reading in September 1972 and contributed data and ideas on Loch Leven. Following this meeting, about 30 scientists from abroad took part in a tour to the English Lake District and Scotland led by P. S. Maitland. The tour visited Loch Leven and various laboratories engaged in the IBP Project. IBP funds to the Project stopped in March 1973 and in June 1973 a symposium on the Loch Leven IBP Research Project was held in the University of Stirling under the auspices of the Royal Society of Edinburgh. Twenty-five papers resulting from this symposium have been published in 1974 as part of the Proceedings of the Royal Society of Edinburgh. A variety of other papers related to the Project are in press or in preparation.

The Nature Conservancy Review of both open waters and peatlands has been completed and will be published (along with the accounts of other habitats) in the near future. The aims of this work were to survey wetland sites throughout Great Britain in order to assess their conservation value and select a group of highly graded sites as potential National Nature Reserves. This work has highlighted just how little is known of the overall quality and structure of wetland ecosystems in this country.

The Wetlands Research Group was also involved in a number of minor projects, among them the study of the distribution and conservation of freshwater fish species. A key to the British freshwater fish was published in 1973. This includes distribution maps for each species. The Group has continued to give advice to Nature Conservancy staff and to answer queries on wetlands problems arising in different parts of the country; it has also advised other bodies such as Planning Authorities.

2. Physical Limnology at Loch Leven

Regular observations of physical factors at Loch Leven have been maintained and are being continued after the official end of the IBP Project. Analyses of the five years of records for the period 1968–1971 will be published in the Loch Leven Symposium volume.

The results of the work on wave action have been published. This work demonstrates the significant effect that wind has on the loch. When a force 8 wind (19 m sec^{-1}) is blowing from the south-west, 12 per cent. of the loch volume is within the shore zone where the action of the waves disturbs the loch bed, while a further 35 per cent. of the total volume is subject to intense turbulence within the wave-mixed layer. As might have been expected, the calculated limit of the shore zone closely follows the sand-mud boundary along the north-east shore and shore area represents about 40 per cent. of the loch bed. The corresponding volumes for a force 5 (9·5 m sec^{-1}) wind are 6 and 15 per cent. of the whole loch.

The work on currents and water circulation within the loch has been continued. The usual analytical approach to lake circulation involves a numerical solution of the equations of motion using a digital computer, a procedure similar to numerical weather forecasting techniques. The effort at Loch Leven has been devoted to developing simpler models, capable of direct solution, that can give some indication of the ecological significance of hydraulic conditions in lakes and how these are effected by wind speed and the geometry of the lake. Preliminary accounts of this work have been written up, but further work is necessary because of the complexity of the systems involved.

(*I. R. Smith*)

3. Ecology of the Phytoplankton at Loch Leven

(a) *Plan of the work*

Estimates of the phytoplankton crop and component population densities have been made at regular (weekly) intervals; these data were then compared with information on environmental factors and experiments designed to test hypotheses were based on the observed relationships.

(b) *Main results*

(i) 1971 observations

A very dense crop, consisting of mainly the diatom *Cyclotella pseudostelligera*, developed early in the year; the maximum of approximately 240×10^6 cells. l^{-1} (equivalent to 240 ug chlorophyll *a*. l^{-1} and containing 5·3 mg C and 9 mg Sio_2. l^{-1}) was achieved before the end of February. The water temperature had not exceeded 4°C by this time.

The collapse of the population brought to an end, temporarily at least, a phase of phytoplankton activity characterised by high population densities and observed algal production rates (e.g. 0·5 g C. m^{-2}. d^{-1}) and a predominance of nanno (>15 um) species. In the late spring and summer of the year the phytoplankton was sparse, and water clarity as indicated by Secchi disc readings, reached 4·75 m.

Autumnal growth was dominated by the diatom *Asterionella formosa* with cells very significantly longer than those of this species observed in earlier years.

This increase in water clarity followed by a netplankton development was contemporaneous with and partly attributed to a very marked increase in the numbers of the herbivorous filter-feeding zooplankter, *Daphnia hyalina* var *lacustris*. This cladoceran was not recorded in the loch from 1967 to mid-1970 and then only in small numbers for a further year. (It was present in Loch Leven at the turn of the century and at least until the late 1950's—see Morgan 1970, *Hydrobiologia*, 35; Walker 1970, M.Sc. Thesis, Univ. of Stirling.) The zooplankton in 1967–1971 was dominated by a copepod acknowledged to be essentially a carnivore—*Cyclops strenuus* var *abyssorum* Sars.

(ii) 1972 and 1973

Full-time studies on the loch stopped in December 1971 but chlorophyll analyses and cell counts were made on samples collected by Mr G. A. Allison, Mrs L. Britton and Mr A. Lyle throughout most of the following two years. Much of 1972 and 1973 were taken up with analysing and writing-up the field and experimental data collected in 1968–1971 (Bailey-Watts, 1973, *Ph.D. Thesis, Univ. of London;* Bailey-Watts and Lund, 1973, *Biol. J. Linn. Soc.*, 5; Bailey-Watts, in press, *Proc. Roy. Soc. Edinb.*, B, 74).

The main conclusions are, firstly, that the shallow, isothermal and nutrient-rich nature of the loch allow the rapid development of high algal crops. Secondly, maximum population densities may be determined by limiting nutrients, even though in the case of e.g. silica, considerable amounts come from the deposits. Thirdly, competition for similar nutrients from other green plants e.g. macrophytes and benthic algae, appears rarely to be important. Finally, utilisation of living algal cells in the water column by grazing Crustacea and Protozoa, or parasitising Fungi, is meagre (cf Bailey-Watts and Lund, 1973, *Biol. J. Linn. Soc.*, 5). The lack of an important grazer may account too for the predominance of small algae—a feature not characteristic of rich lakes (but see below).

(c) *Other investigations*

In October 1972, factors affecting the changes observed in the levels of dissolved and particulate forms of silica were investigated; at that time processes redistributing silica in the loch (diatom growth, sedimentation, frustule dissolution and the release of dissolved silica from the sediments) were much more important than the processes involved in the inflow and outflow of silica to and from the loch. Further investigations of diatom-silica relations are in progress.

Following a preliminary assessment of the 1972 and 1973 data, some comments (Table 4) may be made on the gross nature of the phytoplankton succession in the years prior to 1971 when *Daphnia* was absent compared with that of the years after 1971; (*Daphnia* present). Prior to 1971 the largest increases of algae occurred in the first six months of the year, although the timing and species composition of the various maxima and minima varied (see previous report). In 1972 and 1973 the yearly maxima and highest increases occurred in the second half of the year. In addition, after 1971 the annual averages of chlorophyll *a* concentrations were less than in the previous years. However, in all years nannaplankton predominated over netplankton in terms of species and cell numbers.

TABLE 4. Gross features of phytoplankton succession at Loch Leven during 1968–1970 (*Daphnia* unimportant) and 1972–1973 (*Daphnia* important)

Feature	*1968–1970*	*1972–1973*
Spring growth	Dense crops between February and June	Comparatively low population densities
Summer growth	Poor—period of year when water is at its clearest and chlorophyll *a* concentrations lowest	Dense crops—mainly gas-vacuolate blue-green algae—*Anabaena affinis*, *A. circinalis* and forms of *A. flosaquae*—none of which had been recorded since 1968
Autumn to winter growth	Varied but less dense than spring crops	Very high population densities—centric diatoms (*Cyclotella comta*, *C. pseudostelligera* and *Stephanodiscus rotula* in 1972; small *Cyclotella* ?*stelligera* in 1973)

(d) *Future work*

It is hoped that phytoplankton work on Loch Leven will continue; in particular if measures could be undertaken to prevent the increased eutrophication of the loch (e.g. by reducing the nutrient loading), preliminary large scale experiments could be started as a follow-up to the small-scale work already carried out. Investigations are still necessary into the relative importance of biological and chemical factors, the first perhaps reducing algal biomass, and the second perhaps limiting its increase.

(*A. E. Bailey-Watts*)

4. PRIMARY PRODUCTIVITY AT LOCH LEVEN

(a) *Phytoplankton*

Measurements of photosynthetic productivity by phytoplankton (using the oxygen light and dark bottle technique) and the monitoring of related factors (including crop density (chlorophyll *a*), water temperature, *p*H, alkalinity, dissolved oxygen and carbon dioxide, incident and underwater light intensity) were described in the previous triennial report.

During 1972, data from four years (1968–71) were analysed and sent to the IBP for use in its world-wide assessment of productivity and controlling factors in aquatic and terrestrial environments. Detailed results, and discussions of factors controlling phytoplankton productivity at Loch Leven, are in press (Bindloss, 1974, *Proc. Roy. Soc. Edinb.*, B, 74) and in a Ph.D. thesis about to be submitted to the University of Edinburgh. Some of the major results and conclusions are summarised below.

Hourly and daily rates of gross photosynthetic productivity showed marked seasonal changes within the ranges 0·02 to 1·59 g $0_2/m^2$.h and 0·4 to 21·0 g $0_2/m^2$.h day respectively. Annual gross production values were 1·9 kg $0_2/m^2$.y

for 1968; 2·6 for 1969; 2·3 for 1970; and 1·6 for 1971. In general, gross rates were high compared to values published for other temperate lakes. The higher values observed at Loch Leven approximated those more commonly recorded in tropical and subtropical or in mass outdoor algal cultures.

High gross productivity was facilitated by the generally high chlorophyll *a* content per unit area in the euphotic zone which often approached its estimated theoretical upper limit (430 mg/m²).

The photosynthetic capacity of the algae (i.e. their rate of photosynthesis at light-saturation per unit content of chlorphyll *a*) showed a general tendency to increase as water temperature increased, but appeared to be depressed when population density was high. Field and laboratory evidence indicated that reduction in photosynthetic capacity could be attributed in part at least, to the high *p*H values (up to *p*H 10) produced by photosynthetic CO_2; depletion at high *p*H was shown to be greater than predicted from classical *p*H/alkalinity calculations. The possible influence on photosynthetic capacity of other population density-dependent factors (including nitrogen and phosphorus supply, light history, dissolved oxygen concentration) were also examined, but the available evidence was considered inconclusive.

Zero or negative values for nett photosynthetic productivity were frequently obtained when 24-hour respiration losses in the water column were subtracted from daily gross photosynthetic gains. Such results were considered anomalous since they often coincided with periods of population increase and with dissolved oxygen and *p*H values above those expected at air-equilibrium. Under-estimation of gross photosynthetic due to photochemical oxidation, photo-respiration or the use of stationary bottles could not account for these anomalies. The assumption that respiratory rates, measured near mid-day, remained constant over 24 hours may be in error and may have led to over-estimation of daily respiratory losses. The contribution of bacteria and zooplankton to the measured respiration rates is also a likely cause of over-estimation of algal respiratory activity. Further work on algal respiration is planned.

Consideration was given to the possibility that self-shading (i.e. self-imposed light limitation) and self-imposed high *p*H values may be the critical factors limiting nett production and maximum crops at Loch Leven. If this were true, further enrichment of the loch with nitrogen and phosphorus might not produce higher maximum crop densities, though clearly it could prolong their duration. Further work is planned to assess the relative importance of light, *p*H and nutrient limitation.

The photosynthetic quotient (i.e. the ratio between C_2 evolved and CO_2 taken up) was investigated in the laboratory, using *p*H changes to estimate CO_2 uptake. The quotient appeared to vary with the duration of the experimental exposure period. Its possible variation with the nutritional status of the algae may be investigated in the future.

(b) *Benthic algae*

The rate of photosynthesis of benthic algae was measured in the laboratory using the oxygen light and dark bottle method and sediment samples suspended in filtered lake water. Attached and non-attached algae from two stations of different depth (0·65 m and 1·85 m) were used. In general, the photosynthetic capacity of the benthic algae was lower than that of the

phytoplankton. Light-saturation was achieved at similar light intensities for benthic algae from the two depths as for the phytoplankton. Despite the fact that the benthic algae are confined in nature to regions of lower light intensity than the phytoplankton, they did not appear to be more susceptible to inhibition by high light intensities.

The effect of *p*H on photosynthetic rate of benthic algae was investigated. High *p*H values (up to 9·7) were recorded in July and August 1971 within the macrophyte beds on the north-east shore of the loch. These high *p*H values were shown to reduce benthic algal photosynthesis. Photosynthesis was 63 per cent. higher when sediments from the macrophyte beds were suspended in filtered water from the centre of the loch (*p*H 8·5) instead of in water from above the sediments (*p*H 9·6). A similar (*ca* 50 per cent.) increase in photosynthetic rate was obtained when CO_2 was used to reduce *p*H from 9·6–8·5.

(*Miss M. E. Bindloss*)

5. Studies on Aquatic Macrophytes at Loch Leven

A survey of the submerged macrophytes at Loch Leven, Kinross, was undertaken in October 1971 using a drag rake towed behind a continuously moving boat. Two rakes were used, each being dragged in turn along the bottom for one minute and then brought to the surface for the collected plant material to be assessed. The survey was carried out along straight line transects between identifiable points on the shoreline. After each drag the plants were identified and a rough quantitative measure was made according to whether the rake was either fully laden, more than half laden, less than half laden but more than one quarter laden, or less than one quarter laden.

The survey showed that considerable changes had occurred in the composition and distribution of the submerged vegetation since the previous survey of Polland in 1966 (unpublished). In 1966, submerged vegetation was very sparse over the entire loch, only *Chara aspera* occurring at all frequently. This species occurred in 42 per cent. of the samples, but no other species was found in more than 3 per cent. of the samples. In 1971, by contrast, 41 per cent. of samples contained *Potamogeton filiformis* and *P. pectinatus* and 13 per cent. contained *Zannichellia palustris*, with *Chara* in only 21 per cent. of the samples. Repeat surveys by other workers in 1972 and 1973 confirmed that these trends have continued, and that submerged macrophytic vegetation now forms a small but important part of the primary production at Loch Leven. Further details of this work, including quantitative estimates of the biomass of *P. filiformis* in 1972 and assessing long term changes in the submerged aquatic flora of Loch Leven since the 19th century, are given in Jupp, Spence and Britton (*Proc. Roy. Soc. Edinb.*, B74, 195-208).

Emergent vegetation was very sparse at Loch Leven in 1970–73 and the evidence suggests that it has declined considerably within historical times. Work has been done to assess the present status of emergent vegetation at Loch Leven and to find which factors may have caused this decline. This is planned as a prelude to the re-establishment of vegetation in suitable areas.

In 1972, only 5 per cent. of the shoreline and less than 0·01 per cent. of the area of the loch was occupied by emergent vegetation, the principal species being *Phragmites australis* and *Polygonum amphibium*. The production of *Phragmites* was estimated from standing crop measurements made by harvesting random quadrats within the three major stands which occur at the

loch. The maximum aerial shoot biomass varied from 1·14 to 0·51 kg/dry wt/m² which is low for a eutrophic lake. The estimated total production of all emergent vegetation at Loch Leven was insignificant when compared to other sources of primary production.

Experimental plantings of *Phragmites* showed that grazing by wildfowl, particularly mute swans (*Cygnus olor*) was important in preventing the spread and re-establishment of this plant. Wind and wave damage were also important limiting factors on the exposed shores on the north-east side of the loch where experimental barriers of sand-bags were constructed. Considerable growths of *Polygonum amphibium* covering 1,372 m² subsequently grew in the shelter of one such barrier, while in an unenclosed control area growth of this species was restricted to a few scattered stands occupying only 200 m². One experimental reed bed of *Phragmites* was also established within a wildfowl proof cage in a relatively sheltered area, and the growth of this will be monitored and the project extended in the future. This work was reported in greater detail in Britton (*Proc. Roy. Soc. Edinb.*, B74, 209-218).

(*R. H. Britton*)

6. Benthic Invertebrate Fauna at Loch Leven: Shallow Water

The work on the shallow water zoobenthos in Loch Leven described in the previous triennial report has continued. As in 1970, the sand area of the loch was divided into three major zones for sampling purposes during 1971; within each of these, 24 points were chosen at random and a pair of cores was taken at each point. This procedure was repeated regularly during 1971 from January to December (more frequently in summer than in winter). Of each pair of cores, one was preserved in 4 per cent. formaldehyde for population estimates while the other was kept fresh for studies of the insects that would emerge from it.

The cores retained for emergence studies at each sampling session were grouped in sets of 12 (two comparable sets from each of the three strata) and placed in containers with *ca* 20 cm water overlying the substrate. These containers were taken back to the laboratory at Edinburgh, where they were supplied with constant aeration. Cone emergence traps were fitted over them. Insects emerging from the cores were attracted by overhead lights into the traps, which were emptied every 2–3 days. The insects (which were almost entirely chironomids) were then killed, dried, stored and subsequently identified. The cores from each sampling session were retained not only until the following session but until the day preceding the next session after that. Thus at any one time after the start of the study there were two sets of six containers being run in parallel. The technique has proved extremely successful and considerable numbers of adult chironomids of a variety of species were collected, mainly from April to September. These are proving very valuable for taxonomic purposes, and will also give some information on temporal and quantitative aspects of emergence from sand in Loch Leven.

A paper on the sediment/benthos survey carried out in 1968 is being prepared for publication. A general paper on the zoobenthos has been completed and is in press. In this paper the available information, both published and unpublished, on the zoobenthos of Loch Leven has been studied and tabulated. There have been a number of major changes in the community over the last 100 years—notably a reduction in diversity of the

fauna with the disappearance of many species of invertebrates, particularly Ephemeroptera, Odonata and Coleoptera. The existing macro-invertebrate fauna is dominated by larval Chironomidae, but Nematoda, Mollusca, Annelida and Crustacea are also important. Dramatic changes have taken place in the chironomid population during the present study (1968–71), notable among which has been the disappearance of *Endochironomus*. Production studies of the two dominant larval Chironomidae (*Glyptotendipes* and *Stictochironomus*) in the sandy littoral area (42 per cent. of the loch bed) gave annual estimates of 40·5 and 1·2 g (dry weight)/m² respectively for 1970 and 5·0 and 10·2 g/m² for 1971 (Table 5). Speculative estimates of the entire zoobenthos production in 1970 gave a value of 46·5 g/m².

(*P. S. Maitland*)

TABLE 5. Production estimates for 1970 and 1971 based on Allan curve data for *Limnochironomus*, *Glyptotendipes* and *Stictochironomus* (A=1st generation, B=2nd generation in each year)

	Limnochironomus		*Glyptotendipes*		*Stictochironomus*	
	mg/m²	*J/m²*	*mg/m²*	*J/m²*	*mg/m²*	*J/m²*
1970 A	137	3,067	9,643	212,917	313	6,326
1970 B	457	10,232	30,876	681,742	893	18,048
TOTAL	594	13,299	40,519	894,659	1,206	24,374
1971 A	163	3,650	2,557	56,459	483	9,761
1971 B	221	4,948	2,463	54,383	9,737	196,785
TOTAL	384	8,598	5,020	110,842	10,220	206,546

7. BENTHIC INVERTEBRATE FAUNA AT LOCH LEVEN: DEEP WATER

Annual production of larval Chironomidae in the mud was measured in areas of water down to 10 m over the whole loch from March 1971 to March 1972. The Chironomidae were the most abundant group of the zoobenthos at Loch Leven and were major food items for fish and tufted duck (*Aythya fuligula*). This work formed the final phase of an IBP field programme which was preceded by investigation into methods of measuring production of benthic animals in 1968–70, and by trial measurements of production within a section of the deep water in 1970–71, both described in the previous report. The principal objective of the final phase was to measure production by four species of Chironomidae (which accounted for at least 75 per cent. of the production by this group). The study was also designed to measure production by some smaller and less abundant species and to use the data, together with other biological and physico-chemical information, to look for relationships between the growth and abundance of some species of larval Chironomidae at different points in the loch and the characteristics of their habitat. This would be a preliminary examination, possibly leading to management orientated studies on factors controlling the food of fish and wildfowl.

This study covered 662 ha of the loch or about 50 per cent. of its area. This was divided geographically into seven equal sized sections. Sampling points were chosen at random from the 378 squares of 0·25 ha forming each section. Thus during each sampling session a series of stratified samples was taken to give mean estimates of the abundance and body weight of each species of

larva. A Jenkin mud corer was used for this, fitted with a tube of 7 cm internal diameter. Six sites were sampled in each of the seven sections. Six cores were taken at each site; five of these cores were bulked and used for production estimates and one retained for other measurements. Fifteen sets of samples were taken at fortnightly intervals between May and August, extending to three months in winter.

The samples were sieved using meshes with apertures of 175 μ which retained virtually all larvae. Samples taken in May and June, when many small larvae were present, were subsampled to reduce sorting. Larvae were initially separated from inorganic mud by flotation in a sucrose solution and removed from other organic material and identified under a dissecting microscope (×10—×40). The larvae were oven dried at 80°C and weighed on a microbalance. Samples from four species of larvae were used to determine energy equivalents and ash content and these analyses were carried out by the Nature Conservancy chemistry unit at Merlewood.

Some other information to support the main study was also gathered in 1971. To measure growth rates of enclosed populations of larvae, samples of 0·25 m^2 of mud were taken with a large pneumatic grab (designed by this team) and placed in ventilated boxes within the loch. Growth of larvae was found to be similar inside and outside these boxes. This showed that the production estimates were not likely to be influenced by large-scale movements of larvae with different rates of growth. Also, samples taken by this grab were placed in shallow water and fitted with traps to catch adult Chironomidae as they emerged. These were used for taxonomic purposes to assist in identifying the larvae.

Production of *Chironomus anthracinus*, *Glyptotendipes paripes*, *Polypedilum nubeculosum*, and *Limnochironomus pulsus* was estimated by numerical rather than graphical methods. All these species were univoltine, with adults emerging from May to early July. For the period between each sampling session, production was calculated from the average number of each species present multiplied by the weight increment of individuals. These results are summarised in Table 6 which shows that *Chironomus* was the most abundant, with a cumulative production about 15 times greater than was found in other species. Most production occurred from April–May and from July–September. In the first period there was a marked increase in the average weight of all members of the 1970–71 generation except *Glyptotendipes* (Fig. 7). In the second period, the 1971–72 generation was growing very rapidly and the cumulative production increased exponentially at this time. Weight losses occurred in all these species from November to December resulting in negative production at that time. Nett production for these four species totalled 29 g/m^2 (579 kJ/m^2). Confidence intervals could only be given on these results during a period when there were no young larvae entering the population, because in incrementing populations mortality had to be estimated by indirect methods. In Chironomus cumulative production from 20 July 1971 to 21 March 1972 was 19·1 g/m^2 for which the estimated 95 per cent. confidence interval was ±6 per cent. The equivalent figures for *Limnochironomus*, which was much less abundant and more unevenly distributed than the previous species, were 0·36 g/m^2±0·09 g/m^2 or ±26 per cent. These estimates were within the values predicted and were adequate for the purposes of this study.

TABLE 6. Summary of production and of component data for four common species of Chironomidae from deep water between March 1971–March 1972

	Numbers	*Weights*	*Biomass*	*Production*	*Production*
	Average Nos./m²	*w dry (mg) (mean individual weight)*	*B dry (g/m²) (mean Biomass)*	*P dry (g/m²/year)*	*Energy (kJ/m²/year)*
Chironomus	9,043	0·72	6·53	25·7	515
Glyptotendipes	368	1·77	0·65	1·7	38
Polypedilum	783	0·18	0·14	0·6	13
Limnochironomus	1,028	0·14	0·15	0·6	13

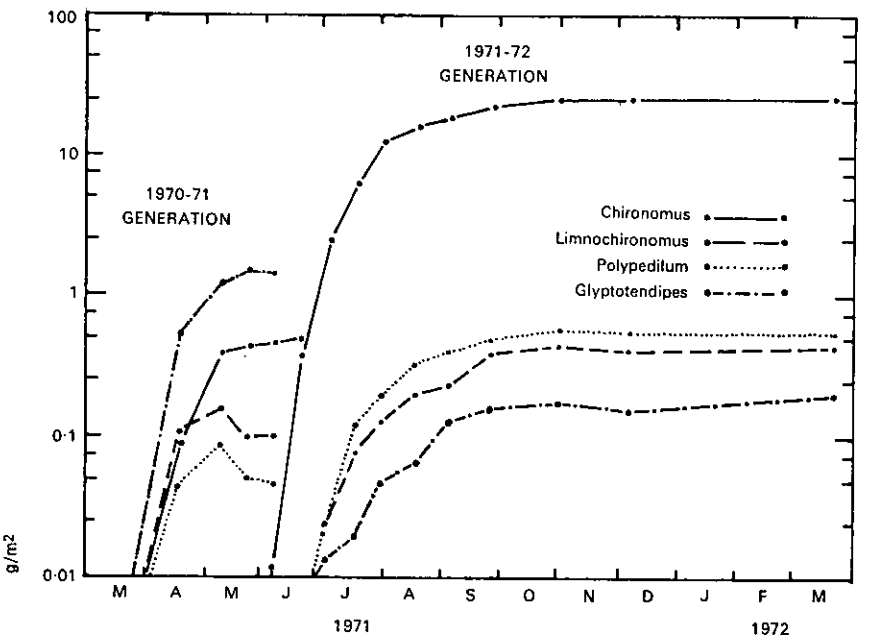


FIG. 7—Cumulative production by each generation in four species of larval Chironomidae in deep water between March 1971 and March 1972.

Sixteen species of larval Chironomidae were identified from the deep water during this study, plus a few Orthocladiinae and Tanytarsini, which were not identified fully. Apart from the Chironomidae described above, the Tanypodinae were the most important group in terms of numbers and production and were represented by four common species. Nett production for all Chironomidae between March 1971 and March 1972 was approximately 34 g/m², which was slightly higher than the figures reported from most other rich temperate lakes. Using published data (McFarlane & McLusky, 1972 *Comp. Biochem. Physiol., 43*) on respiration for *Chironomus*, *Glyptotendipes* and *Polypedilum*, assimilation by this predominantly phytophagous larval community was tentatively estimated at 1,700 kJ/m²/year.

The results of this study were presented at the Loch Leven Symposium and the production estimates obtained in 1970–71 were given at the Fifth International Symposium on Chironomidae at Abisko in Swedish Lapland. Subsequently, the sorting and identification of the Tanypodinae were completed and the estimates of production are being prepared for publication. Also, the construction of the pneumatic grab has been written up for publication, and the production data are being analysed to assess relationships between the characteristics of larval populations and the habitat in different parts of the loch.

(W. N. Charles, K. East, T. D. Murray)

Jenkins corers in use on the Nature Conservancy catamaran at Loch Leven sampling chironomid larvae in the mud.

8. General Physical Limnology and Survey

Many aspects of physical limnology involve the consequences of water movement, a rather neglected topic compared to other elements in the underwater climate. A simple account of fluid dynamics and its application to limnology has, therefore, been prepared and is now in press.

For a few weeks in 1972, observations were made on the hydraulic conditions in Lake George, Uganda, the site of the Royal Society's African IBP PF Project. The climatic difference between Loch Leven and Lake George provided some very instructive contrasts. Compared to the normally isothermal Loch Leven, Lake George, which is almost 19 times greater in area and yet little more than half its depth, has a regular daily pattern of afternoon stratification. A joint paper (with Dr A. Viner) was contributed to the Symposium on the Lake George Project in February 1973.

Following completion of the work concerned with the IBP aspects of Loch Leven, the basis has been started for a study of regional comparative limnology for all British standing waters. The objects of this are (*a*) to provide a physical back-ground for biological survey work, and (*b*) to provide rapid estimates of physical conditions in lakes and avoid the need for any observations *in situ*. The first stage involves counting all standing waters occurring on 1 : 250,000 (1 inch=4 miles) maps. Tables, subdivided by Hydrometric Area, giving the grid reference, morphometric and other data, have been prepared and will be transferred to punch cards or tape.

At the same time, simple statistical models are being developed, some as generalisations of work done originally as part of the Loch Leven Project, to permit estimates of physical parameters to be made using data in the original lake census tables. Examples of the information that can be obtained are the mean annual inflow and thus the theoretical retention time, the likelihood of stratification and the extent of wave action.

(*I. R. Smith*)

9. Conservation of Open Waters

In 1970–73, the Conservation Review exercise discussed in the previous report was completed. Ninety-nine open water sites of national or international importance for conservation were listed. Of these, 19 were running water sites, generally entire river systems, while the remainder were standing waters ranging in size from small ponds to some of the largest lakes in Britain. Most of these sites have now been scheduled as Sites of Special Scientific Interest and negotiations are proceeding for the declaration of National Nature Reserve status on some of them. The criteria for the selection of sites and the survey methods used in the exercise are described in the previous report.

Survey work with the aim of assessing the scientific interest of sites for conservation has continued during the present period, during which a number of sites missed in the original Conservation Review exercise have been examined. The methods of the original exercise have been used in these follow-up surveys. In addition, a few of the sites listed in the Conservation Review which have been altered since the original survey have been re-surveyed in more detail. These include, for example, Llangorse Lake, Breconshire, a shallow eutrophic lake subject to intense recreational pressure. Here, emergent and submerged macrophytic vegetation have been surveyed and regular monthly samples of zooplankton, phytoplankton and water for chemical analysis have been taken.

Advice on the conservation and management of open waters was given to the Nature Conservancy and other bodies interested in the conservation of wetlands. Generally, the advice consisted of predicting the likely effects of

proposed developments on the ecology of open water sites of known conservation interest (usually SSSIs). Developments which have been considered included reservoir construction, road schemes, sewerage schemes, recreational developments, and the use of herbicides and piscicides. Sometimes the effects of such schemes comld be predicted from information in the literature, but often field survey was required to assess the situation where any development had been carried out. It was the practice, whenever possible, to monitor the site before and after the event to test predictions. One such example is Attenborough Gravel Pits (Local Nature Reserve), Nottinghamshire, where a proposal was made to breach the banks of the polluted River Erewash in order to reach gravel deposits on the opposite bank. The site was monitored for a period of a month before the breach and for a year thereafter. The breach caused a predicted large rise in phosphorus and nitrogen concentrations within the gravel pits where NO_3–N concentrations reached 8·0 mg/l and phosphorus 1·5 mg/l. These extremely high nutrient levels led to very heavy algal crops, but although partial deoxygenation occurred near the breach and the benthic fauna here consisted mainly of pollution tolerant species such as *Tubifex tubifex*, the flora and fauna of the remainder of the pits remained relatively intact.

Advice was also given on the construction of new waterbodies and the assessment of their conservation potential, and on the planting of new waters with suitable aquatic plants. A key to the vegetative characters of aquatic plants together with notes on habitat requirements has been prepared in collaboration with other workers. This will be published in 1974.

(R. H. Britton)

10. Conservation of Rare Fish Species

The collection of records of the distribution of all freshwater fish species in the British Isles has continued and existing maps are being up-dated where necessary. Work on rare species has continued and active measures are being taken with two of these (the Lochmaben vendace, *Coregonus vandesius*, and the burbot *Lota lota*) to conserve the British stocks from extinction.

The vendace project was described in the last triennial report and continues. In 1973, netting was carried out both in the Mill Loch, Lochmaben (the sole remaining site for the Lochmaben vendace) and in the Galloway lochs (to which eggs were introduced in 1968). No fish was caught during any of these nettings. A small stock was shown, however, to be present by netting in a small pond near Glasgow, into which fry had been introduced in 1970. Reading of scales from the fish caught has shown that the original stock bred there in 1972, and it is hoped to rely on these fish in 1974, when a major attempt to obtain fertile spawn will be made.

Work on the burbot has been limited so far to laboratory rearing of young fish to determine if this species can successfully be brought to sexual maturity in captivity. If this can be shown to be the case, then it is probable that the most useful approach to handling the small remaining British stock will be to obtain wild specimens and collect fertile spawn from these in captivity. Growth of the fish in laboratory conditions has so far been rather slow and it is likely that outdoor ponds will be necessary to achieve complete success with this and a number of other species.

(P. S. Maitland, K. East)

11. Peatlands

During the past three years the Nature Conservation Review was completed and the work has changed. The main emphasis now is on describing and explaining the variation in British mires, through a detailed investigation of a number of selected sites. It is hoped to present the results as a monograph. Advisory work on site assessment, conservation and management has continued.

The sites selected for survey give a wide geographical range, and include examples of the main structural types defined in the more general survey for the Nature Conservation Review. In all, 60 sites are being sampled, and 30 are receiving particular attention. At all sites a description of the main morphological characters and broad vegetation zones is accompanied by vegetation records from 40 randomly placed quadrats (1 m^2). Analysis of the results will show the range of plant communities and their relationships to one another, whilst at the same time demonstrating the diversity within single sites. Within the 35 sites more detailed morphological, stratigraphical (using published material or contracted outside experts), floristic, chemical, hydrological and land use information is being collected, together with available documentary evidence of past land use. This will relate the present vegetation to existing environmental conditions and developmental history. Peat depths and surface contours are being plotted, peat samples for chemical analysis are being collected at six-monthly intervals, and water-table depths and their fluctuation ranges are being measured. Within basin and valley sites the floristic composition of transect lines is being recorded to illustrate variations in zonation of communities, whilst in all types of site shorter transects are being used to show either patterns of transition from one community to another, or the effects of microtopography on floristics. Due to lack of expertise, no co-ordinated scheme for investigating animal populations is included within the project.

Several smaller projects are also in hand, including monitoring successional changes and the effects of specific management operations. Most of these are only in their early stages and no results are yet available except in the case of rehabilitation studies at Malham Tarn Moss where the object is to find a method of restoring an active *Sphagnum* surface on the raised bog. Shallow pools (20 cm deep) have been formed by removing peat and replacing the surface mat of vegetation in small experimental plots. Small amounts of aquatic and semi-aquatic *Sphagnum* have been introduced and preliminary results suggest that the plots will be quickly colonised to form *Sphagnum* carpets. Other projects include the study of water table fluctuation at the Silver Flowe and Inverpolly. Linked with this, a preliminary hydrological investigation of the research site at Inverpolly was carried out by Mr C. J. Keegan (an M.Sc. student in Civil Engineering, Birmingham University).

There has been a substantial amount of advisory work, of three main types. Requests for an assessment of the effects of specific development proposals were the most numerous. These came from the Nature Conservancy and from Local Authorities. Other requests have been for conservation evaluation of peatlands in areas where large-scale development is taking place, e.g. afforestation in Wigtonshire and developments associated with the oil industry in Shetland. This type of evaluation has also been required for Local Authority Structure Plans. A third type of advisory work has been the formulation of

management plans for peatland nature reserves at the request of regional staff and various outside bodies. Among bodies to whom such advice has been given are Monmouthshire County Council (Cleddon Bog), Cheshire Conservation Trust (Danes Moss), Scottish Wildlife Trust (Flanders Moss), Fisons Ltd (Thorne Waste, Yorkshire), Field Studies Council (Malham Tarn Moss). Numerous requests have also been received from Nature Conservancy staff for guidance on the management of peatland nature reserves.

(*D. A. Goode, R. E. Daniels, E. M. Field, T. D. Murray*)

Other Work on Vertebrate Populations

D. Jenkins

1. Introduction

This group is concerned with problems of population dynamics in some birds, with building up programmes on predator/prey relations, and with the effects of afforestation on wildlife. The emphasis is on vertebrates not covered by the Grouse Team or the Range Ecology Group, but closely integrated with them. Dr Jenkins' own research has been on aspects of population dynamics in waterfowl, chiefly shelducks in co-operation with Dr Patterson of Aberdeen University, with students in two departments at Edinburgh University, and with Dr Goss-Custard of the ITE Coastal Ecology Research Station. This work is of basic interest in aiming to understand how the numbers of this bird are controlled, and if the bird numbers are adjusted to the estuarine food supply. Dr Jenkins and Dr Newton also worked together actively with the Nature Conservancy Council on the population dynamics of mute swans in the Outer Hebrides; the data are now being analysed. Dr Newton's main work is on birds of prey, and especially the factors controlling the numbers of sparrowhawks and the effects on sparrowhawks and their prey of changes in afforestation. This involves first getting precise information on what wildlife there is in forests of different sorts, and some ideas on biological productivity. The project has developed in conjunction with the Forestry Commission who supplied assistance in the nesting season each year, and with Glasgow University where analyses are done for pesticides. Dr Newton also supervises a Ph.D. student in the Department of Forestry and Natural Resources at Edinburgh University. Research on buzzards developed jointly with the Royal Society for the Protection of Birds, with the aim of getting basic data on the natural factors affecting numbers and dispersion, and the hen harrier project dove-tails with the grouse studies. It aims to get basic data on population processes in this raptor, but particularly to get facts about harrier predation on red grouse. The group also contains two DAFS scientists as integral members, and arrangements were successfully reached for financial assistance from, and thus a joint project on foxes with, the Forestry Commission. Mr Hewson also co-operated in a joint programme on mountain hares with the REG. The newest recruit to this research group is Dr Harris whose very wide previous experience of sea-birds has brought him actively in contact with workers in this field throughout Britain and also in many other parts of the world.

2. Research on Wildfowl and Sea-Birds

(a) *Population dynamics of shelducks in east Scotland*

This project, which began at the end of 1966, continued in my spare time. The aim was to understand the population dynamics of shelducks at Aberlady Bay where numbers of resident birds have been similar each year since 1967. The biggest advance in the last three years has been finding a technique for catching birds for marking them. Previous efforts with a clap net failed, but 66 full grown birds were caught in 1972–73 using the drug Avertin (under licence) on wheat as bait, and others were caught on the nest or as ducklings.

Study of these birds confirmed that non-breeders as well as breeders were resident, and showed that a few adults which did not breed in one year had done so in previous years. Altogether there were about 105 breeders and about 25–45 non-breeders each year.

Breeding was poor in most years, with 44 per cent. of known nests deserted through natural causes in 1973. Fledging success was also poor, with the number of young per old bird fledged in late July reaching only 1·2 in the best year and 0·09–0·4 in the other years. Poor hatching and poor fledging were both attributed to the effects of high density. The fact that not all adults bred, and the stability in numbers of both breeders and non-breeders despite variable breeding production, together suggest that the number of adult birds resident in the Bay was regulated. The idea is that numbers were brought up to a constant level each year through immigration.

Interest centres on the way in which this supposed regulation is brought about. The birds held territories from March onwards, but the same total number was recorded each January and the population divided into potential breeders and non-breeders before the territories were taken up. The mechanism regulating total numbers and dividing the birds into breeders and non-breeders is thought to centre on the birds' feeding ecology and behaviour. They fed chiefly on *Hydrobia ulvae* and other invertebrates which burrow in the sand and mud. These animals were most abundant in the mud sediments along the stream, less so in the silts near the head of the estuary and scarcest in the sand near its mouth. The hypothesis is that the number of birds that settled in the Bay depended on their interactions with each other. They are thought to have competed for feeding space, possibly with the extent of rich feeding area on the mud setting a limit to the number of breeders and the extent of the poorer silts setting a limit to the number of non-breeders. Thus the amount of feeding space in late winter is held to be the critical resource limiting numbers, with the birds that obtained feeding space subsequently dividing the whole Bay between them to form territories. On this argument, territorial behaviour was a result of the regulating process rather than its cause. The next step is to devise suitable experiments to test the hypothesis.

I was helped by Mr Philip Hall in 1971 and by Mr Martyn Murray in 1973 who worked on shelducks for the field projects done as part of their undergraduate courses in the Departments of Forestry and Natural Resources and Zoology at Edinburgh University. These two students did all the work on the sediments and invertebrates at Aberlady Bay, and also helped greatly with counting and catching birds and with developing ideas about the social structure of the population. A new student project by Mr Gordon Armstrong of the Department of Forestry and Natural Resources began in late 1973 on the dispersion of the marked birds within the Bay.

(*D. Jenkins*)

(b) *Reasons for the decline in puffins*

When the English and Welsh populations of puffins *Fratercula arctica* declined in the middle of this century concern was aroused but no long-term study initiated. However, when it was realised that the larger north and west Scottish colonies, whose puffins constituted 15–20 per cent. of all British seabirds, had also, and more recently, diminished in size, the present work to discover the reasons was started at the end of the 1972 breeding season.

Although a very obvious bird, the puffin is difficult to census because of its large numbers, the isolation and rugged nature of its breeding places and the widely fluctuating attendance of adults and immatures at the colonies. Counts of birds are of very limited value. The only practical way to monitor breeding populations is to set up permanent transects and quadrats in grassy colonies, to count the occupied burrows year by year, and to try to relate these counts by comparing rates of fish-carrying adults coming to different areas at the same time to colonies in boulder screes where nests are completely inaccessible. Such transects are now set up at five main puffin colonies.

On the east of Scotland, the much smaller puffin population is increasing. The Isle of May had less than ten pairs in 1955, now it has several thousand. Ringing and retrapping has shown that many of these Isle of May puffins are immigrants from the large Farne Islands colony (100 km south). Conditions must be very favourable, and the ecology and population dynamics are being studied there for comparison with those of the declining colonies. This comparison should pinpoint the weak link in the life-cycle of declining populations, and show whether it is a failure of eggs to hatch, young to fledge, or a high mortality of immatures or established breeders. Not until this is known can a reason for the decline be sought in the environment.

The only colony definitely declining *at present* is that on the Shiants (in the Minch) where numbers of pairs breeding in sample areas have declined from 21,900 in 1970 to 8,890 in 1973 (Cambridge University Expeditions). However, when I started work there in May 1973, it was immediately obvious that black rats *Rattus rattus* were eating so many eggs that the chances of uncovering any more widespread reasons were remote. Such other influences must exist, because other colonies (e.g. St Kilda, North Rona) have declined in the absence of rats. Despite the rats, 27 young were successfully reared from 68 eggs laid in study burrows. Although this 39 per cent. success was much lower than the 63 per cent. found on the Isle of May, it could still be sufficient to keep the breeding population stable. Later in the season, work was switched to St Kilda. This is a more difficult island to work, but at least it is free of rats. There it appeared that young were short of food late in the season, and that which was brought in by the adults was atypical. This could be the first clue of the underlying problem.

Eggs were collected at several colonies and analysed by the Toxic Chemicals Unit at Monks Wood. Since the highest residues were mainly from the Isle of May birds, organo-chlorine residues have almost certainly not been responsible for the declines on St Kilda and the Shiants.

TABLE 7. Toxic chemical residues in puffin eggs in 1973

		Mean concentration ppm in crude extractable fat		
Locality	*No. of eggs*	*PCB*	*DDE*	*dieldrin*
St Kilda	7	35·1	8·57	<0·7
Shiants	6	25	5·30	<1·0
Isle of May	14	<50·0	6·46	<1·51

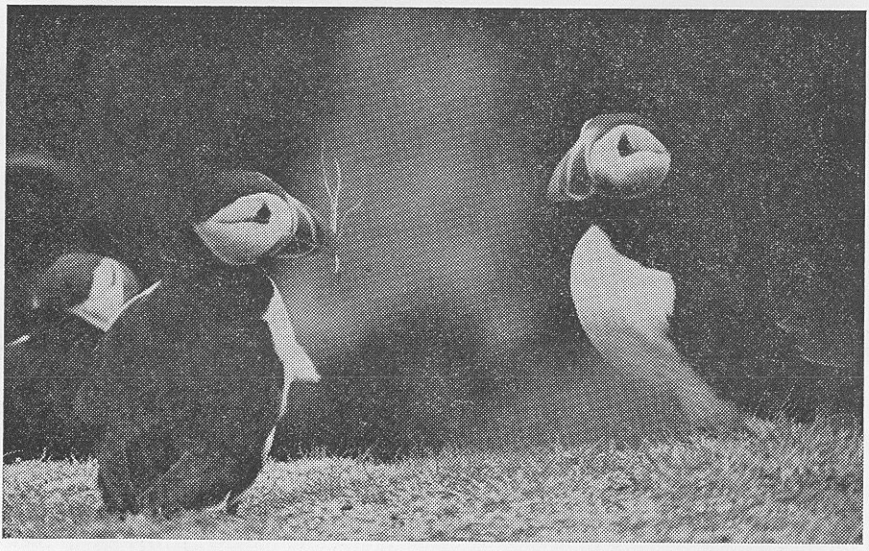
The ultimate cause for the decline is likely to be found away from the colonies but the wintering grounds are unknown. The low recovery rate of ringed birds and the wide scatter of recovery localities (Newfoundland to

Italy) suggest a pelagic distribution at low densities. Cruises in February and October on RRS Shackleton in north-eastern Atlantic from Britain south to Madeira and Cape Verde Islands failed to find any puffins off the Continental Shelf. Further voyages to the central Atlantic and western Mediterranean are planned.

An intensive ringing programme is underway to find where puffins die, or at least get washed ashore. This is linked with a colour-ringing scheme which indicates the colony where ringed, breeding status and age (if known). In 1973, birds were thus marked on the Isle of May (1,100 individuals), St Kilda (1,000), the Shiants (1,500), Fair Isle (600) and lesser numbers on the Farnes and in Sutherland. This work is to be extended, as preliminary results suggest that puffins are far less faithful to their natal colonies than most other seabirds. The possibility of some of the birds from declining colonies having moved to the increasing colonies cannot be ruled out but the losses far outweigh the gains. The loss of perhaps a million or more puffins during the last few decades still has to be accounted for.

In addition to the main study, the use of aerial photography as a means of assessing and monitoring cliff-nesting seabirds is being investigated.

(*M. P. Harris*)



Puffin carrying material to line nest-chamber.

3. Research on Vertebrate Predators

(a) *Research on sparrowhawks* (*Accipiter nisus*)

The aim of this research is to find what is currently limiting the numbers and nesting success of sparrowhawks in different parts of Britain. Until organo-chlorine pesticides came into widespread use, this species was common throughout Britain and, despite heavy persecution from game preservers, maintained its numbers well. But it has laid thin-shelled eggs, with a consequent reduction in nesting success, since 1947 when DDT came into wide

usage; and suffered a massive population decline from 1955, when the more toxic cyclodiene compounds (aldrin, dieldrin, heptachlor) came in. Following successive restrictions since 1962 in the use of these latter compounds, however, the species has in some areas begun to recover, but is still nesting with reduced success.

Natural densities of sparrowhawks

A first step was to find at what densities sparrowhawks bred in well-wooded areas, where they were depleted neither by shortage of nesting places, nor by heavy pesticide usage. Normally, the same nesting places were used year after year, each being occupied by a succession of birds. In ten well-wooded areas in different parts of Britain, nest-sites were regularly spaced; but the distances between sites, and hence the maximum breeding densities, varied greatly between areas. For example, in the woodlands of Annandale (Dumfriesshire) nest-sites were about 0·6 km apart, in the Dee Valley (Kincardineshire) they were about 1·1 km apart, and in the Spey Valley (Inverness-shire) about 2·4 km. These gave densities in continuous woodland of one pair per 0·4 km^2 in Annandale, one pair per 1·6 km^2 in Deeside, and one pair per 6·8 km^2 in Speyside. From earlier records, the locations of nest-sites, and the differences between areas, were found to be consistent over long periods of years. They were related to differences in the biological productivity of different areas, and hence probably to the abundance of small-bird prey, an idea which is being tested. In each area, year-to-year fluctuations in breeding numbers caused year-to-year variations in the proportion of sites occupied.

Effects of pesticides on nesting success

From 386 nests found in Dumfriesshire in 1971–73, 167 (43 per cent.) failed to produce young. Almost all the failures were of the types associated with pesticide contamination, namely non-laying (having built a nest), egg-breakage and embryo deaths. Moreover, in 300 unhatched eggs collected for analysis, substantial levels of organo-chlorine compounds were found, mainly DDE (a metabolite of DDT), PCB and some dieldrin. Particularly striking was the great range of variation in residue levels found in clutches from one 770 km^2 area (53–700 ppm in yolk fat), but among eggs from the same clutch, variation was slight. Differences in levels between clutches were linked with differences in their success. Clutches showing 'normal' success contained significantly less residue, on average, than clutches showing partial success, and less again than clutches that failed completely. Among complete failures, the highest levels were in eggs that were incubated, yet failed to hatch; intermediate levels were found in clutches that failed through breakage; and the lowest levels in clutches that were deserted.

Egg-shells collected in 1971–73 weighed 17 per cent. less, on average, than shells collected in the same general area in 1900–45, before organo-chlorine compounds came in. Most breakages in 1971–73 occurred in clutches with the thinnest shells; and the degree of thinning was related to the amount of DDE in the egg. These findings provide further circumstantial evidence for the involvement of organo-chlorine compounds in causing breeding failures in sparrowhawks, and show that egg-breakage, though widespread, is not the only important pesticide-induced cause of failure.

How much the reduced breeding success affected adult numbers is not yet known, but population trends will be followed for further years to find how these relate to pesticide levels in eggs. The sensitivity of the sparrowhawk makes it a good indicator of organo-chlorine levels in the terrestrial environment; and interestingly the species is still absent from the most heavily cultivated (=contaminated) parts of south-east England.

(*I. Newton*)

(b) *Numbers and growth of sparrowhawks in relation to food supplies*

In an attempt to find how numbers of sparrowhawks related to numbers of their prey, populations of song-birds were censused in plantations and woodlands in two areas where sparrowhawk nesting densities differed markedly: Annandale (Dumfriesshire) and Speyside (Inverness-shire). Two counting techniques, the repeated mapping of singing males and the line transect, were used and evaluated in 1973. Total bird densities in Dumfriesshire plantations were of the order 400–600 pairs/km^2. In comparable habitat in Speyside they were only one-third as great. The line transect method produced results of unacceptably high inconsistency. Much greater reliance could be placed on the mapping technique. The relative vulnerability of woodland prey species to sparrowhawk predation was also assessed. Large species, such as the chaffinch (*Fringilla coelebs*) were taken more frequently in relation to their numbers than were small species.

Growth of young sparrowhawks was studied at 16 nests in Dumfriesshire. Development was described qualitatively, and daily measurement made of weight, tarsus length, first primary feather length and amount of food in the crop. Growth rates were highest, and food in crops consistently greatest, at nest sites within 1 km of farmland, and at sites in small woods compared with large afforested areas. The markedly larger females grew significantly faster than males from an early age. This project has run for one year, and will be continued.

(*D. Moss, Ph.D. Student*)

(c) *The behaviour of the sparrowhawk*

Sparrowhawk behaviour was studied by casual observation for three years near Banchory, Kincardineshire. Hens were seen more often than cocks throughout the year. Cocks were more often disturbed from a perch and hens more often seen flying above the canopy. Display was most common in March and May. It was usually preceded by high soaring and was more frequent in hens than in cocks. Obvious interactions between birds occurred rarely but were of three types: a close association of circling birds; chasing each other (cock and hen); and diving with the presenting of talons (hen to hen). No cock to cock interactions were seen. It seems that high soaring itself might be a display, and that hens (not cocks) defend an area around the nest site.

Variation in the visibility of sparrowhawks with sex and season would complicate the use of sight records to detect differences in population density or sex ratio between areas.

(*M. Marquiss, Ph.D. Student*)

(d) *Numbers and breeding success of buzzards in Speyside*

The aim of this study, which took place mainly in 1969–72, was to investigate the role of social behaviour in determining the numbers and spacing of buzzards. This species was particularly suitable for such a study as it was known to be territorial throughout the year. Although once common in the Spey valley study area, the buzzard was persecuted so severely by game preservers that by the end of the last century it was rarely seen and did not breed. It recolonised the valley in the 1940's. By mapping all our observations of territorial birds and their conflicts with their neighbours each year from 1969, we found that territory boundaries remained almost unaltered from year to year, even when birds were replaced. Territories did not overlap by more than 10 per cent. and most were discrete. About half the study area was unoccupied by pairs and when new territories were formed they were usually in this ground, although there were exceptions. Some immature and unpaired adult buzzards defended small territories in winter on parts of the unoccupied ground. In summer unpaired birds did not defend territories, but hunted mainly in unoccupied ground adjacent to existing territories and occasionally even attempted to live within existing territories. Most colour marked young left the area after dispersal, but some returned and took territories in their second year.

Our study of the buzzards' breeding during the four seasons showed that the mean clutch size ($2{\cdot}96 \pm 0{\cdot}72$; $n=72$) and fledged brood size per successful nest ($2{\cdot}56 \pm 0{\cdot}81$; $n=80$) were higher than previously recorded by any comparable study in Europe. The mean number of young fledged per successful nest was highest on average in territories which contained the greatest amount of farmland. This may have been because the major prey species of the buzzard (e.g. rabbits, voles and ground-nesting birds) were most abundant and relatively easily hunted in farmland.

(*D. N. Weir, N. Picozzi*)

(e) *The relationship between hen harriers and red grouse in Deeside*

Apart from the intrinsic interest of the relationship between a predator and its prey, my study of hen harriers (*Circus cyaneus*) is also an applied problem. Grouse moor rents are at record levels, and harriers are often persecuted despite protective legislation. However, there is absolutely no information on how predation by harriers during the summer affects the numbers of grouse available for shooting in August. I aim to find out. The practical problems involved in such a study are considerable, particularly the very big areas used by the birds and the fact that first year birds and adult females are brown and hard to see.

A feasibility study in 1970 and 1971 enabled me to establish a satisfactory working relationship with the gamekeepers on the study area and to develop the necessary expertise to count harriers and to find their nests. This made it possible to define the project in terms of two main aims:

(i) To determine the density at which an undisturbed population of harriers would stabilise on a grouse moor.

(ii) To study the effect of harrier predation during the summer on red grouse.

(i) The number of actual harrier nests on a moor is not necessarily the same as the potential since some nests may fail. So I had to find a way to count potential breeders. The best way to do this seems to be to watch for displaying birds in spring and to follow up each pair in turn for any evidence of nesting. This approach showed that adults in spring were irregularly distributed over the study area with pairs based on known or assumed nest sites approximately 2·5 km apart. Certain parts of the moor were favoured for nesting, though apparently not all were used each year. The reasons for this are not known. Even if all were occupied, the density would still be less than half that of harriers on the Mainland of Orkney, and the relatively low density may be due to persecution on neighbouring estates or to natural causes. So far, up to one-third of my pairs failed either to complete their nests or to hatch their eggs. Most of the breeders that failed then left the study area. More years of study are required to find whether the numbers of pairs will stabilise at about the present low level or fluctuate, perhaps in relation to the previous breeding success.

(ii) In 1972 and 1973, detailed observations were made from a hide at one nest each year. This was the only satisfactory way of establishing which were the preferred prey items. Meadow pipits (*Anthus pratensis*) were the most numerous, followed by grouse chicks (one-third of all prey) and young hares and rabbits (*Oryctolagus cuniculus*). When corrected for weight, grouse chicks represented approximately two-thirds of the diet of the young harriers. Observations of the adults showed that the minimum hunting range was 1,400 ha and that it could be as much as 2,000 ha. Counts of grouse in late

Hen harrier feeding young, Kincardineshire, July 1972.

summer on areas regularly hunted by harriers and on irregularly hunted control areas showed that the young to old ratios were not significantly different from each other. In this study period, grouse stocks were high and bred well. Thus there were plenty of grouse for both harriers and sportsmen. We need to know what proportion of the grouse stock is taken by a natural stock of harriers in a poor grouse year, and my programme will continue in the hope of getting such a poor year.

(*N. Picozzi*)

(f) *Research on foxes in Scotland*

Although the extent of predation by foxes on sheep has nowhere been satisfactorily established, farmers expressed misgivings about the ban on the use of the gin trap in Scotland in April 1973, claiming that an increase in foxes would result. Accordingly it was necessary to include, early in any research programme, attempts to assess the present status of foxes in Scotland and the methods used to control them. Data were available on the numbers of foxes killed by grant-aided Fox Clubs and under bounty schemes from 1948–1970, and by the Forestry Commission from about 1961 onwards. Broken down into eight main geographical regions these showed that:

(i) in east, central and south Scotland numbers of foxes killed increased to 1955/56, then declined sharply and remained low for several years before beginning to rise towards pre-1955 numbers. In Argyll there were no such fluctuations.

(ii) the big decline occurred when myxomatosis reduced the rabbit population. Reproductive success was low in 1956, but then returned to normal. Foxes in Argyll may feed mostly on field voles and sheep carrion and so would be affected less by myxomatosis.

(iii) good reproductive success in 1951 was associated with late and heavy snowfalls and abundant carrion.

(iv) foxes spread into parts of north-east Scotland, where they were previously unknown, from about 1960.

(v) in recent years the proportion of cubs to adults killed has gone down, which suggests that density-dependent factors may be involved.

A survey carried out by DAFS Field Officers and 93 Forestry Commission rangers in 1971/72 showed that foxes were killed mostly in snaring. Only in the Highlands, where gin traps were set at pools, were these the most used control instrument. The same survey collected data on damage by foxes to farm animals. In Argyll more lambs were alleged to have been killed in flocks below 500 ewes than in bigger units, so that a management factor may be involved. In the crofting counties twice as many farmers reported losses as in the rest of Scotland.

Work on reproduction, age structure, and food of foxes, based on the examination of substantial numbers of carcases, was begun in 1971 and will continue for several years. Analysis of prey remains in over 500 fox scats (droppings) collected in Argyll and the north-east showed that field voles occurred more often than other prey in Argyll, with marginally more sheep and deer remains in scats from the open hill than in scats from forests. Rabbits and hares were the main food in north-east Scotland. Attempts are

being made to assess the food available for foxes in west Scotland by an annual index of vole populations, and by counting sheep carcases in selected areas and observing the rate at which they are broken up by scavengers.

No satisfactory method has been devised of estimating numbers of foxes. One possible approach is to map occupied fox dens each year in various study areas to compare densities between areas and between years. This work is done by DAFS Field Officers in conjunction with gamekeepers at about a dozen places in Scotland; it is hoped to increase these to thirty.

In April 1973 a study of sheep losses in relation to the number of occupied fox dens was started in Lochaber, in conjunction with Mr J. Anderson, DAFS Inverness. More than twenty farmers are co-operating by keeping detailed records of numbers of sheep and lambs, and several also marked lambs so that losses could be studied in detail.

Dr H. H. Kolb was appointed to the fox project in November 1972 and Mr J. Anderson has assisted part-time from early 1973.

(*R. Hewson, H. H. Kolb, DAFS*)

Nature Conservancy Council
Sub-Regional Office

J. A. Forster

During most of the period under review the executive and research functions relating to nature conservation in Britain were contained within one organisation, the Nature Conservancy of the NERC. In November 1973, the Nature Conservancy Council Act 1973 resulted in two new bodies, The Nature Conservancy Council undertaking the executive function and the Institute of Terrestrial Ecology, the research function. Recognising the important interactions between research and management in nature conservation, it is the express wish of Government that close links be retained between the two organisations and indeed, where appropriate, the organisations will continue to share offices and facilities. Thus within the Institute of Terrestrial Ecology at Brathens the East Region of the Nature Conservancy Council retains a sub-office covering the counties of Aberdeenshire, Kincardineshire and Banffshire.

The work of the Nature Conservancy Council falls broadly speaking into two categories. The first is concerned with the acquisition and management of National Nature Reserves, and the second is an advisory role on all issues relating to wildlife conservation.

There are five National Nature Reserves in the sub-region, the mountain reserve of the Cairngorms, the newly acquired birchwood of Morrone near Braemar, the small oakwood at Dinnet and the coastal areas of Forvie and St Cyrus. The management of each reserve is undertaken according to a plan designed to conserve the scientific interest. The plan for Forvie NNR has been revised during the period and hence particular attention has been given to its management problems. In common with many coastal areas it is being increasingly used for recreation, and careful management is needed to regulate this so as to protect the disturbance to wildlife. Other recent problems have been the post-myxomatosis build-up of the rabbit population, which has repercussions not only for the management of the vegetation communities but also on the NCC's relations with neighbouring occupiers of land, and the disturbance caused to valuable tern and eider duck colonies by foxes.

Much of the NCC's advisory role is exercised through consultations with the local planning authority over Sites of Special Scientific Interest. Within each county the Conservancy submits to the planning authority a schedule of these sites and it is then consulted on the implications of any development proposed. The schedule for Aberdeenshire was recently revised so that there are now 44 sites in the county. The rapid economic growth of the north-east, largely associated with the exploration and production of North Sea oil and gas has brought a marked increase in development cases referred to the NCC. One of the most notable was the case of the Loch of Strathbeg, a site of outstanding importance for its freshwater biology, dune ecology and ornithology where plans to bring a pipeline through the site to an adjacent gas terminal were successfully opposed by the NCC and local ecologists. Elsewhere, close consultation with the planning authorities, and liaison with

landowners and other government agencies such as the Forestry Commission and Department of Agriculture, has avoided damage to any scheduled sites.

In addition to the site casework there is an increasing and welcome trend for the NCC's advice to be sought on the implications for nature conservation of a wide range of countryside developments, and for the opportunity to be given for the NCC to contribute to local planning studies. For example the NCC provided substantial information for the Aberdeenshire County Council study of the county's coastline. The NCC is represented by an assessor on both the Aberdeenshire and Banffshire Countryside Committees.

Nature conservation can only be based on knowledge of the distribution and abundance of plants and animals and of the ecological implications of particular management operations. In future, research into the ecological basis of conservation will be sponsored by the Nature Conservancy Council through contracts placed with the Institute of Terrestrial Ecology and other bodies, but this will not take the place of the direct contact by local NCC officers with research workers which has proved so fruitful in the past.

Commentary on Ecological Research and Land Use

I. A. Nicholson

Instances can be cited in Britain and throughout the world of the way knowledge of ecological processes has affected land use and management. Nevertheless, it is sometimes held that the impact of ecological science on land use in this country has been disappointing.

It would be unwise to dismiss this implied criticism and attribute the cause entirely to economic and political factors which are always involved. On the contrary, many ecologists would themselves express disquiet at the prevailing situation. The approach to research, no less than the ecological base of land use in relation to current knowledge, requires continuous review. This offers the best prospects for promoting ecological influence and for helping to ensure that new insights are incorporated into the ongoing process of economic planning. This level of planning can affect whole regions and establish the framework in which decisions by individuals are made on policy and day to day management; and hence the nature of the influences on the countryside. An indirect form of state planning through various financial measures has been commonplace for many years, while a particularly topical case of planning at this level is represented by proposals under Common Market arrangements for mountain and certain other areas.

Today we may be at the threshold of a long period of flux, which could offer many opportunities to re-examine land use questions. It is therefore appropriate to review the role of ecology and its impact, and to examine some of the underlying reasons for the present status of ecology, with special reference to land use in upland Britain.

In the last report in this series I drew attention to the tendency to view our mountains and moorlands in a fragmentary way from the standpoint of the different economic uses and nature conservation. Since then the Report of the Select Committee on Scottish Affairs (Land Resource Use in Scotland) has been published. The minutes of evidence given by private individuals and government bodies strikingly illustrate this fragmentation and its consequences. While value judgements are bound to affect the polarisation of opinion, it is disturbing that the existing substantial scientific base in ecology, and its associated specialisms, is apparently inadequate to provide a greater concensus amongst scientists on matters of land resource use.

Research orientation

A large body of work in ecology is now problem-orientated. Comparatively little research in what is traditionally regarded as ecology is done under the aegis of agriculture and forestry organisations, though a great deal of work in specialised aspects of the subject might be included under the heading of ecology, depending on the definition that is adopted. The greater proportion of government sponsored research in ecology in the traditional sense has been done within a framework of nature conservation.

Eighteen years ago Sir Frank Fraser Darling wrote: '. . . ecology must come out of its academic shell and help in the investigation of problems affecting our survival. Ecology will lose nothing of its scientific spirit in embracing

problems of communities dominated by man; indeed, by such studied enlargement of its field, the science should be a corrective to much of the technological, pragmatic experimentation which loses sight of the initial and constant aim of science, to find truth.'* While in the past two decades there has been a clear trend in the direction advocated by this author, a substantial body of ecology has developed as a science applied to nature conservation. Thus, the intellectual atmosphere in which much ecological work has been conceived, with the exception of work in some academic institutions, has been strongly influenced by thinking concerning the conservation of nature in its own right, though in recent years problems posed by environmental abuse of direct and immediate importance to human life and health have attracted increasing attention. On the other hand, problems underlying the intelligent exploitation of natural resources and their conservation, including soils, have received less attention than their importance demands.

An example of a practical problem of this type which should legitimately come within the scope of ecological enquiry and expertise can be found in one of the objectives of forest policy (*Hansard*, 24 October 1973): 'Within our limited land surface and the increasing pressures upon it the Government are concerned that forestry should form part of a really effective pattern of rural land use, in which it is harmonised to the best possible advantage with agriculture and the environment.' This problem—and it is of a type that is very common—cannot be resolved through the use of data obtained as a by-product of research having other though related applied aims: it is one that requires an appropriate orientation of research effort. By this I do not imply that a series of *ad hoc* studies would be adequate, but rather that basic understanding is needed of the pattern and other properties inherent in the natural environment and of the principles that should govern the synthesis of the land use pattern that is superimposed upon it.

Research approach

Problems of research orientation are paralleled by those of certain aspects of the approach to much ecological enquiry. Illuminating differences are revealed when the approach in this field is compared with that found more commonly in research associated with the economic uses such as forestry and agriculture. In these, great emphasis is placed on the importance of understanding biological mechanisms with the ultimate objective of controlling them to optimise selected characteristics of primary or secondary production. This is accompanied by a rigorous experimental approach and in certain kinds of work the level and intensity of treatments may go beyond those that would interest the ecologist in analytical studies. By contrast, many wildlife ecologists are less interested in understanding production processes in depth and more concerned with describing relationships amongst organisms as they occur in the field, particularly in situations considered to be 'natural', the concept of a diverse and balanced natural system being the underlying point of reference.

Thus the approach of workers in agriculture, for example, while leading to a profound understanding of certain organisms and of those parts of the environmental fabric of immediate concern, may lead to an inadequate evaluation of the wider implications in time and space. On the other hand,

*F. Fraser Darling. Pelican in the Wilderness. Allen & Unwin, London, 1956.

wildlife ecology may be characterised by comprehension at a broader and more generalised level, but with a less specific understanding of the consequences of changes in the structure of the existing system, or of ways in which compensation may be made. There are strengths in both approaches and there is clearly a case for combining them in the investigation of problems over a broad field.

The concept of a natural system as a point of reference can be particularly misleading when applied to the British uplands because their qualities of 'wilderness' give a false impression of their natural status. Particular examples of the uplands show features that relate to conditions that were more widespread when human influence was less ubiquitous and intense, but plant and animal life, and soils, have been under such heavy pressure from human activities that the concept has little meaning. Moreover, it may channel thinking into an unacceptably narrow framework. Indeed, it is not uncommon for an ecologist to be expected to do *ad hoc* research with the aim of 'improving' an existing system, despite the fact that its basic structure may be palpably unsound.

It is more constructive to consider the present system of plant and animal life as just one expression amongst many that the environment is potentially able to support. Once the environmental capability is understood it is then a matter for decision to encourage those systems that for one reason or another are judged to be the most desirable. Such an approach points to the need not only for an understanding of the biological processes involved, but of the input/output relationships of the alternatives available to provide the basis for choice. It emphasises the positive role of ecological knowledge in its application to the synthesis of systems whose properties (outputs) can be evaluated.

Wildlife ecology still tends to suffer from the inadequately developed relationship between the general ecologist and specialist in disciplines relevant to deeper understanding of many problems. However, the experimental study of selected processes in depth under controlled conditions is increasingly being combined with the more traditional approach of field observation and measurement. The need for the greater use of the experimental method at all levels is increasingly recognised, though the difficulties and cost involved are sometimes limiting. Developments in this direction are essential for improving the capability of ecological prediction, but understanding of processes must be translated to the spatial dimension of land use. To do so there must be a systematic description of the nature of the environment—topography, land form, soil and vegetational distribution and its pattern, as well as the relationships that occur. For a long time this aspect of ecology, as essential for the development of the science itself as it is for its application, has lacked impetus in Britain. In the absence of such background data, the gulf between the understanding of ecological processes and their logical application to land use problems cannot be bridged. In fact where grazing animals are involved, with their mobility and their propensity for environmental impact, it can be particularly hazardous without it to attempt to do so.

Holistic view of ecology

One of the strengths of the ecological approach is the holistic view for which it stands. Theoretically, this should enable ecological understanding

to be applied with particular effectiveness to land use problems, and it must be emphasised that in many ways the existing capability has hardly been exploited. Even so, many of the current disagreements amongst ecologists are due directly to the paucity of quantitative data. The ability for qualitative interpretation and projection in field situations has been outstripped by the need for dealing in more quantitative and specific terms.

The claim that ecology does in fact foster the holistic view would carry more conviction if there were clearer evidence that this view stemmed from a corresponding approach to the whole research process. Thus, I argue, three aspects of this process and their integration require close scrutiny. First, there is the need for a more critical approach to the analysis of ecological processes conjointly with other disciplines. Secondly, the parallel requirement of a rigorous and systematic description of environmental variables and their ecological significance needs to be much more fully catered for in research programmes. Thirdly, problems of interlocking cause and effect that are everywhere apparent have overtaken the traditional methodology in important areas of research. The understanding of such problems could be facilitated by a more effective exploitation of the techniques of systems analysis selectively as an integral part of the overall approach.

The uplands

The proportion of research that should be encouraged to operate with a given orientation, as distinct from the more open ended remit, is a matter of judgement between the competing requirements in catering for the foreseeable versus the unforeseeable. However, the importance of recognising the need for well integrated effort in the land use field is fully established by experience of past inadequacies, and equally by the implications of the growing pressure on land resources. In this respect the problems of the uplands and mountain areas cannot be regarded as unique, but scale and slow response to positive measures of control underline the importance of consolidating in land use systems those influences which are likely to be most beneficial in the long term, and which promote rather than limit flexibility for future use. Moreover, while management based on high inputs may be justifiable in regions where biological activity is high, understanding of how to exploit low inputs in exercising control is, I suggest, the key to the rational development of land use in the greater proportion of the more extreme environment of upland Britain.

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