The Nature Conservancy Research in Scotland

Report for 1968-1970

THE NATURE CONSERVANCY
NATURAL ENVIRONMENT RESEARCH COUNCIL

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The Nature Conservancy
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Edinburgh
EH9 2AS

1970

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H. H. Kolb (N.E.R.C.), terminated 30 September 1969
A. N. Lance (N.E.R.C.), commenced 1 February 1968
K. Laughlin (N.E.R.C.), commenced 1 September 1968
M. Marquiss (Aberdeen University), commenced 1 October 1970
C. J. Savory (N.E.R.C.), commenced 1 October 1968

Introduction

D. Jenkins

This is the first report produced in this form by Nature Conservancy research staff in Scotland. It replaces contributions formerly made in Annual Reports produced by the Nature Conservancy, the last of which was published for the year ending 30 September 1964. Subsequently, short reports on the Nature Conservancy's research in Scotland have been included in the general accounts of the work of the Nature Conservancy published in the reports of the Natural Environment Research Council. The most recent of these was for the year ending 31 March 1970. A policy of publishing three-year reports on the work of the Nature Conservancy's research stations has now been adopted, and this report gives a more detailed account of the work of staff based in Scotland for the three years up to 31 December 1970, with some reference to the earlier period since the last Conservancy report.

Organisation

The organisation of the Nature Conservancy in Scotland has differed from that in the rest of the country where there are several research stations to which regional conservation staff are attached. In Scotland, all Regional Officers and some Deputies have been based at Edinburgh, together with the Land Agent, his staff and the Administrative Group. Until 1966, all Nature Conservancy research staff in Scotland, except the Unit of Grouse and Moorland Ecology, were also based at Edinburgh headquarters. The Grouse Unit was located at Blackhall, Banchory, and administered by Aberdeen University.

In 1967, however, it was decided that a new Mountains and Moorlands Research Station would be built at Banchory, and in anticipation several additional members of staff were posted to Blackhall. In the event, money for the building was not available until 1970 but work has now started on a site at Brathens Hill, about three miles north of Banchory. The original Grouse Unit was wound up in 1968, and all its staff were taken on by the Nature Conservancy.

The Wetlands Research Group, based at Edinburgh, was formed in 1966 with the main objectives of co-ordinating the Conservancy's programme of research on wetlands and participating in the activities of the International Biological Programme at Loch Leven, Kinross. In this research, the Conservancy team is part of a larger group with members in several universities and other government laboratories, supervised by a committee composed of prominent limnologists. Also based at Edinburgh are those botanists and zoologists of the Range Ecology Research Group for whom there is not yet accommodation at Banchory. The Range Ecology Group was formed in 1968 with the aim of co-ordinating work on Scottish uplands by scientists who formerly worked separately. This group also co-ordinates the activities of the Conservancy's Mountains and Moorlands Habitat Team (a composite group promoting liaison between Research and Management in this habitat). Its main research activities are the study of relations between soils, plants and grazing animals in uplands, and between the major land uses

and wildlife. The Range Ecology Group will all be based at Banchory when the new station is finished. The Predator Research Group was started in 1969, as a development from the Assistant Director's Laboratory. It is based partly in Edinburgh, with work in south Scotland on sparrowhawks, and partly in Banchory with work in Deeside and Speyside on crows, hen harriers and buzzards. This group works very closely with an officer of the Royal Society for the Protection of Birds. A scientist of the Department of Agriculture and Fisheries for Scotland is to be appointed on 1 April 1971 to work on foxes from Banchory and to liaise with the other workers on vertebrate predators. Research on waterfowl ecology and management has also been directed from this laboratory. An Assistant Regional Officer is based at Banchory, and one experimental officer from the Range Ecology Group is outposted to Aviemore.

Staff

The total staff in Scotland is 122, with 62 at Edinburgh headquarters and another 60 outposted in the regions. Of these, 48 are engaged on research, including the Assistant Director's personal secretary and the station secretary at Banchory. Altogether there are 20 scientific officers, 26 supporting staff including three stalkers, and the two secretaries. The groups and their heads are as follows:

Grouse	Dr A. Watson
Predator	Dr D. Jenkins
Range Ecology	Mr I. A. Nicholson
Wetlands	Mr N. C. Morgan

Largely due to its origins as a Unit in Aberdeen University, and also partly because it is the oldest and best established group, the Grouse Team has a tradition of incorporating research students as essential members of the group. This tradition has worked successfully and so far there have been nine students for Ph.D. degrees and one for an M.Sc. degree. Several of these students have been supervised by the Assistant Director. In 1967–70 there have been five postgraduate and one undergraduate student in his laboratory. Two other research students have worked with the Range Ecology and Wetlands Research Groups. 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

T. D. Murray	Scientific Assistant, 1 October 1968.
W. J. Jenkins	Scientific Assistant (temporary), 1 October 1970
C. O. Badenoch	Assistant Experimental Officer, 1 January 1969
R. P. Cummins	Assistant Experimental Officer, 6 October 1969
I. S. Paterson	Experimental Officer, 1 April 1968
R. Hewson	Experimental Officer, 1 July 1968
B. W. Staines	Senior Scientific Officer, 1 October 1968
C. O. Milner	Senior Scientific Officer, 1 May 1970
P. Arman	Senior Scientific Officer, 1 July 1970

Resignations

R. W. Youngson	Assistant Experimental Officer, 30 September 1969

Promotions

R. A. Parr	Assistant Experimental Officer, 1 July 1968
D. A. Goode	Senior Scientific Officer, 1 June 1969
N. G. Bayfield	Senior Scientific Officer, 1 June 1970
P. S. Maitland	Principal Scientific Officer, 1 June 1970

Professor R. Robel (Kansas State University) and Professor D. A. Boag (University of Alberta) visited Banchory during their sabbatical years. R. Moss, I. Newton and A. Watson were in Canada/U.S.A. for periods of ten, ten and three months respectively. R. Moss's visit was in co-operation with the Institute of Arctic Biology and the Alaska Co-operative Wildlife Research Unit. I. Newton's visit to Canada was in exchange with R. H. Kerbes of the Canadian Wildlife Service. A. Watson received a Nuffield Lectureship to Canadian universities. Other members of staff were abroad at conferences and on short visits. Many scientists visited the research stations at Edinburgh and Banchory.

Publications

All the groups in the Research Branch produce mimeographed progress reports approximately every two years. The progress reports give a resumé of research aims, methods and results and are aimed at a readership of scientists working in similar fields and other people who have technical interests in the work done. The triennial reports summarise results and are aimed at a wider readership of conservationists. In addition, a short mimeographed register of all research projects is produced annually. This states the expected duration of each project and lists recent publications. Completed projects are written up in scientific journals, and a complete list of recent publications is given on pages 93–98 of this report.

Public relations

Liaison with Scottish universities continued throughout the period, with particularly good contacts at Aberdeen, Edinburgh and Stirling. Students from all these and other universities have frequently visited the two research stations and their study areas in the field, and members of Conservancy staff have lectured and participated in seminars at the universities. In addition they have trained research students as members of their groups. Recent developments have been 'Open Days' at Edinburgh and Banchory as part of European Conservation Year 1970, with the Banchory 'Open Day' featuring as part of the local show in 1969 and 1970.

This report

Attention is particularly drawn to the following new findings. Good breeding success of red grouse is not necessary for an increase in breeding stock, nor poor breeding for a decrease. Fertiliser experiments indicate that grouse do not make an immediate adjustment of territory size to food quality, but that birds living on the better food for some time do take smaller territories. New experimental work shows that much of the variation in breeding success of red grouse and ptarmigan can be accounted for by

variations in egg quality. An unidentified hormone-like factor present in growing heather stimulates egg production in red grouse. In addition, there is evidence that increased human disturbance and damage to vegetation near ski-lifts in the Cairngorms region has not so far affected breeding stocks or breeding success of red grouse, ptarmigan and dotterel.

In the Range Ecology Group, early work on red deer nutrition is demonstrating the considerable growth potential of young deer and the extent to which current range conditions are suboptimal for growth and development. Studies on the condition and body composition of red deer through annual cycles are laying the foundation for the interpretation of observed gross changes in deer seasonally and of differences in performance in different seasons and in different areas. They also provide a basis for linking nutritional studies on red deer with research on the range. Work at Glenfeshie has demonstrated the value of deer behaviour studies in deciding on the siting of plantation blocks. Studies on the seasonal pattern of deer grazing have shown the importance of juniper for late winter use, particularly in periods of snow cover. In contrast, young plants of birch were particularly severely grazed in spring when the buds burst. The fact that birch plants were not deliberately sought in winter suggests ways of encouraging regeneration without the complete exclusion of deer from an area.

Work on grazing is beginning to establish quantitative relationships between range dynamics and grazing pressure from herbivorous animals, opening up the possibilities of more positive control of range trends. Work on birch woodland has demonstrated the high mortality of young birch after the first year. High seedling establishment was associated with the occurrence of areas of bare soil and patches of compact *Sphagnum*. Subsequently, high sapling mortality is associated with dense woodland canopies and heavy grazing.

Work on burning of *Molinia*-rich blanket bog has demonstrated the short duration of the effect of burning in terms of increased deer use. It has underlined the problem of managing *Molinia* areas and the need to increase the frequency of other plants, e.g. *Calluna*. In research on Cairngorm on an area used heavily for recreation, the main factors associated with damage have been identified. Research on paths has greatly increased our capacity for the rational design of paths in reserves and elsewhere.

The surveys carried out by the Wetlands Research Group for the Conservation Review of both Peatlands and Open Water are the first attempts at a comprehensive coverage such as is necessary to describe the range of variation of these ecosystems in Britain. Although several organisations study fresh waters in Britain, the Wetlands Research Group of the Conservancy is the only one concerned with conservation problems in the wide sense. The Loch Leven study is now the largest main IBP/PF contribution in the United Kingdom. More components of the ecosystem have been investigated than in any other lake in Britain. It is one of the few places in Europe where water movement is being studied in fresh water and the amount of effort going into benthic studies is greater than in most other IBP projects. Particularly, advances have been made in the methodology and statistics of benthos sampling. Another project aims at saving populations of rare fishes threatened with extinction.

A small group now works on predators, especially birds of prey. This new group is a co-operative effort with the Royal Society for the Protection of

Birds, and a scientist from the Department of Agriculture and Fisheries for Scotland will join them early in 1971 to work on foxes. Work on the breeding biology of some ducks has demonstrated a high level of predation following disturbance of the ducks by people; and work on grey geese has defined some points of conflict between geese and agriculture.

Cages for grouse or ptarmigan at Blackhall, Banchory.

Grouse Research Group

A. Watson

1. Introduction

This team is studying how populations of wild red grouse (*Lagopus lagopus*) and ptarmigan (*Lagopus mutus*) are limited, particularly the inter-relationships of populations and behaviour, food, the physical environment and inheritance. It is mainly a fundamental study of population regulation, but also has applied ends and much of the work is directed straight at management. Most research is done on wild birds, but a large captive stock of grouse and ptarmigan is kept for experimental work on behaviour, reproduction, nutrition and inheritance. From 1967 to 1970, A. Watson also led another 'Human Impact' Team which examined the effects of increased human pressures on animal populations, vegetation and soils on the vulnerable arctic-alpine habitat near ski-lifts in the Cairngorms, and studied methods of rehabilitation where damage had occurred. In 1970, this work became part of the research of the Range Ecology Group under the leadership of I. A. Nicholson.

Justification of the research

We are studying one of the commonest vertebrates in a habitat occupying a large part of Britain, and it is important to know more about this ecosystem and how it may be managed. Alternatively, we may justify the research by the people who visit us or write to us, i.e. by the problems that interest them. These are, in order of numbers, the ecologists, shooting men, and human biologists. We are doing a fundamental ecological study of populations, behaviour, nutrition and inheritance in two closely-related species, the red grouse and the ptarmigan. Our understanding of their population regulation is still rudimentary, depending too much on correlations and changes in percentages, and not enough on experiments. The complex relationships of populations, behaviour and food are not yet well understood in any wild animal, and the explanation of population cycles in northern animals is still something that few ecologists agree about. These matters are of interest as fundamental science, but they also have practical applications and a rapidly increasing economic importance for game management, tourist development, recreation and land use in Britain and other countries. Perhaps more important for direct human welfare, intensive studies of spacing behaviour in animals are of increasing interest to those social psychologists, psychiatrists, planners and others who are beginning to study the much-neglected field of man's aggression and spacing problems in mental hospitals, housing flats and elsewhere. There are therefore good reasons for pressing on with research on the populations, behaviour and nutrition of red grouse and ptarmigan.

Our co-operative research in western Ireland is aimed at improving a very wet infertile environment for vegetation and wildlife, and at creating a wildlife resource of economic value in an area with a low standard of living and other serious social problems.

Human impact on vegetation, soils and animal populations near ski-lifts in the Cairngorms is a recent example of a general conservation problem that

is rapidly increasing as more and more people go to the countryside for recreation. The problem of human pressures on wildlife is often discussed but there is a great lack of quantitative descriptive studies and experiments directly aimed at the problem, which is the approach that the Human Impact Team took.

2. Red Grouse Populations

Population Studies

Population data are essential baselines for measuring any changes after experimental treatments of the environment, and for properly understanding observations and experiments on nutrition, behaviour and breeding, in captivity and in the wild.

Several study areas on a rented moor at Kerloch near Banchory are used for a long-term study of clutch size, breeding success, mortality and other population processes, and for experiments such as fertilising and burning. On these and many other areas outside Kerloch, we count grouse to find the sex ratio and the size of the breeding stock in spring, and we assess the adult sex ratio, brood sizes, and age of broods, and mean breeding success (number of young reared per old bird, or young to old ratio).

The size of the breeding stock at Kerloch declined from 1966 to spring 1969, and has increased to spring 1971. Breeding success at Kerloch was poorer from 1966–68 than in earlier years, and was good in 1969–70. The problem is whether this can be largely explained by poorer nutrition for the parents in 1966–68 (data not yet all available) or whether some other associated factor has also to be taken into account, such as the fact that egg-robbing crows (*Corvus corone*) were not killed on Kerloch in these three years. Although 1966 was the worst year for breeding, grouse bred well in that year on a 16 ha fertilised area, with 1·9 young reared per old bird; the best on any other area was 0·6. In 1967, the birds on the fertilised area again did better (0·9 young: 1 old) than elsewhere. Yet the fertilised area was at the edge of farmland and woodland where crows were common, and one pair of crows reared a family alongside the area in both years. The improved nutrition was followed by better breeding success in spite of the presence of breeding crows. Of course this does not mean that crows were unimportant in the absence of the improved nutrition, or that grouse on the fertilised area would not have done even better in the absence of crows, but it does indicate the relative importance of the two factors when both occur together. In the two years running since 1969, the crow stock in spring has been virtually wiped out (p. 85), and no nests of grouse or other ground-nesting birds found by us were robbed, compared with 6–30 per cent. in earlier years. The possibility of egg-robbing by crows as a complicating factor, possibly confusing the influence of other factors on grouse, will be eliminated from now on by killing the crows every year.

On study areas outside Kerloch, the results confirm earlier findings that breeding densities and breeding success are higher and steadier on areas over base-rich rocks than on areas over poorer rocks.

In 1970, the population data on red grouse back to 1957 were re-analysed by the methods of 'key factor' analysis developed by entomologists, including the concept of density dependence. The general conclusion is that, while such methods are a useful way of looking for numerical relationships when the

only data available are counts of animals, they contribute little to our present scheme or 'model' of what are the underlying causal mechanisms of population change in red grouse on our intensively studied areas.

Fertiliser experiment on Kerloch

Calcium ammonium nitrate was spread all over 16 ha of unburned heather in May 1965 at 500 kg per ha, and a nearby control area of 16 ha was left alone. The fertilising was followed by an increase in the heather's growth, nutritive value, and flowering for three years. All grouse were shot by early August 1965 to remove any possible effect on the colonisers from the traditions of the previous residents.

The main conclusions of this experiment are (*a*) that incoming grouse which had been reared elsewhere did not take smaller territories in autumn 1965 on the area of better food than on the unfertilised area, (*b*) that territorial grouse living on the fertilised area subsequently reared larger broods, and (*c*) that the number of grouse taking territories on the fertilised area was greater than on the control area in 1966 and two later years.

Other fertiliser experiments

The fertiliser experiment at Kerloch was designed to test hypotheses derived from field observations, and was not intended as a trial for practical economic management. Fertiliser was spread uniformly over the whole area, with a heavy enough application to provide a clear answer from the experiment. However, as grouse stocks did increase after this experiment, this raised the possibility of improving grouse shooting by fertiliser treatments. This might be economic if grouse were to respond when the fertiliser is spread in patches or strips. We also wished to get some replication of experiments and to test new ideas. Here, fundamental scientific work and the needs of applied management met closely.

In 1968, we began new experiments, co-operating with estates in Perthshire and southern Scotland where the landowners, shooting tenants or Scottish Agricultural Industries paid for the fertiliser and the costs of spreading. The research, involving sampling heather and counting grouse, was a joint project with J. Phillips of Economic Forestry Ltd. All the areas were open to sheep, red deer (*Cervus elaphus*) or cattle, as there seemed little point at that time in trying fertilisers for practical management if one had to put up fences to keep out sheep or deer. Calcium ammonium nitrate was applied in April–early May, varying from all of the ground covered on one area through various intermediate treatments to one width of the fertiliser spreader in every twenty.

Grouse stocks showed no change on any fertilised area as compared with its appropriate control, except on the area given a 1 in 1 blanket treatment. Sheep, cattle and red deer concentrated more on the fertilised than on the control areas, and the obviously heavier grazing on the fertilised strips probably prevented a response by the grouse. (In Ireland, red grouse increased greatly on an area where only one eighth was treated with phosphorus fertiliser, but where large grazing mammals were kept out by fencing.) The cost-effectiveness of the 1 in 1 treatment, in terms of the better grouse shooting and the good price for lambs that both followed, has not been analysed yet.

The 1 in 1 experiment greatly advanced our understanding of grouse population regulation. The result shows that grouse took smaller territories

in autumn on a fertilised area even though breeding success in the same summer was no better than on the unfertilised control area. Taken in conjunction with the Kerloch experiment, it suggests this explanation or model: grouse take smaller territories on fertilised heather if they have been reared on it or have lived there for some time, but not if they are incomers that have settled quickly on the fertilised ground. This in turn suggests that spacing behaviour is affected by plane of nutrition over a period but not by some immediate response or adjustment to the environment.

New experiments with phosphorus fertiliser were begun in 1970 in co-operation with two estates near Forres, using spraying from a helicopter. These will be useful as applied research, and may also show if phosphorus is important in grouse nutrition. If there is an effect on grouse, it is likely to last longer than with nitrogen fertiliser.

If sheep and grouse both respond favourably to fertilisers and the result is economic, particularly in terms of better grouse shooting, then there may be a possibility of large-scale land improvement for grouse and domestic stock, without the high capital costs of ploughing and grass reseeding. Reseeding in any case destroys the habitat for grouse and so ruins the shooting value of the treated areas, and often leads to serious defects for agriculture in the long term. It is also possible that the fertilising of natural moorland vegetation may improve the performance of red deer and decrease their natural mortality.

We want to emphasise that it will be several years yet before we know if fertilisers produce a response by the grouse that is economically worthwhile for practical management. Another important problem is that we do not know yet what side-effects the fertilisers may have on poor moorland soils. It is possible that the long-term effects may be undesirable; for example grasses might oust heather (a possibility with nitrogen fertilisers) and soil fertility might eventually get worse than it was before. For all these reasons it would be premature, undesirable and uncertain economically for landowners to start using fertilisers on a large scale at present.

Burning experiment at Kerloch

A previously neglected hillside of 49 ha, which in 1961 had only three patches of heather less than six years old and had much rank heather, was the experimental area, and a similar hillside with rank old heather was the control. Many patches, none bigger than 2 ha, and equivalent in all to 10 fires per 10 ha, were burned each spring from 1962 to 1965 on the experimental area, and none thereafter. No fires were burned on the control area.

Heather regenerated in the first summer after burning. Breeding stocks of grouse stayed similar on both experimental and control areas for two years, and increased in the third and fourth years on the experimental area, but not on the control. Then, two years after burning ceased, the breeding stock decreased on the experimental area, and by 1968 was down to the previous level before burning started. There are two main points:—

(*a*) breeding stocks increased without an intermediate step of better breeding, and

(*b*) there was no increase until three summers after burning began, numbers were higher for only three years, and a decrease occurred two summers after burning had ended.

It seems that the increase after burning lasts a very short time unless burning is continued every year or two on an area. This suggests that it may not be a good idea to concentrate many small fires on an area within a few years, then move on to concentrate on another area, and so on block by block to cover the whole moor. Probably it would be better to burn fires scattered over the whole moor each year.

(*A. Watson, R. Parr*)

3. Ptarmigan Populations

Fluctuations in breeding stocks of ptarmigan seem to be more regular and of longer duration than those of red grouse on most of the grouse study areas, though the fluctuations of grouse at Forvie are similar to those of ptarmigan. There have been three study areas for ptarmigan, one on very base-poor granite at Derry Cairngorm, one on a slightly more fertile granite at Lochnagar, and a pair on base-rich rocks (a mixture of base-rich schists, limestones and quartzites) at Cairnwell. A fourth pair was added on the very poor granite at Cairngorm in 1967 to study the effects of human impact. Another was used for two years at Beinn a' Bhuird to provide data for C. Summers, an Aberdeen University botany student doing an I.B.P. study of the productivity of arctic-alpine vegetation.

At Derry Cairngorm, the ptarmigan bred well in the years of increase and in the early years of peak numbers, and poorly in later peak years and in years of decline. At Lochnagar and Cairnwell, across the Dee Valley, years of low or high numbers tended to be the same as at Derry Cairngorm, but the exact timing of an increase or decline varied by up to a few years on the different areas. Ptarmigan at Lochnagar were still at a peak in spring 1968 when the stocks at Derry Cairngorm had fallen considerably. At Cairnwell, stocks were high up to 1967, but dropped to about one half in 1968–70. The mean density of the breeding stock over a period of years was higher on the base-rich rocks at Cairnwell than elsewhere, and on average ptarmigan bred more successfully there.

(*A. Watson*)

4. Red Grouse Behaviour

Introduction

In late 1966, we already knew that spring breeding stocks of grouse are determined by the territorial behaviour of the birds in the previous autumn. Our present aim is to find more about this mechanism, asking (*a*) why do the birds choose territories of a certain size and not some other size, (*b*) why does territory size vary in different years, and (*c*) why do some birds fail to get territories while others succeed?

The work involves a continuing study of individually-marked birds on about 160 ha of the lower moor at Kerloch, assessing aggression, mortality, survival, territory size and breeding success, in relation to population changes.

Experiments using hormone implants

In spring 1967 and 1968 we replicated earlier experiments by giving an implant of testosterone to a territorial cock grouse each year. They both became more aggressive and took bigger territories. The 1967 bird had been unmated previously but after the implant it paired up with a hen on some

days. We also gave a territorial cock an implant of oestrogen. This cock consistently had a hen over the winter, but she left him soon after he was implanted. He became less aggressive and eventually gave up his territory. He was seen later, after territorial behaviour had waned greatly with the onset of the breeding season, but did not pair up again and breed.

Strife and aggression

Recent studies indicate that grouse show more strife (more singing, fighting and other agonistic behaviour per bird per hour) at high than at low densities. More strife involves more behaviour that is aggressive, but these birds do not necessarily have more inherent aggression. They may simply be reacting to the closeness of their neighbours. In the first fertiliser experiment, cocks at higher density on the fertilised ground showed more strife than on the control area alongside. However, the cocks on the control area reacted to intrusion at greater distances, and defended larger territories. Thus they were more aggressive in terms of the space they wanted, even though they showed less strife.

Aggression and inheritance

Differences in aggression may be affected by a bird's nutrition and inheritance. In 1968 we began an attempt to study aggression and inheritance in the wild. Our programme involves an attempt to ring, weigh and grade the condition of all grouse chicks on about 200 ha each summer over a number of years. Many of these birds come to our trapping areas in subsequent autumns for individual marking with plastic back-tabs, and later we know which get territories and which fail. We have already found that young cocks take territories within a very short distance of where they were hatched, competing with their brothers and fathers and even replacing their fathers as owners of pieces of heather moorland. A. Lance (p. 18) has also found this with a smaller sample of birds, but with more detailed information about each individual, from his telemetry study of several families.

The number of young reared by a pair is an inadequate basis for discussing selection, although it is often wrongly used in the scientific literature for speculative arguments about natural selection and family size. Instead, the crucial information is to find the proportion of these young (*a*) which become territorial, (*b*) which rear offspring (i.e. F_1) and then (*c*) the proportion of these offspring that become territorial, and so on to future generations. By intensive marking, it may be possible to study the fates of families from one generation to the next, and to know if grouse that are aggressive, or have big territories, or belong to a particular year-class, or have poorer or better food available, are more successful in contributing to future generations than other birds. If these attempts in the field are successful, they raise the possibility of studying the inheritance of aggression, and the genetic structure of local populations and of different social categories of grouse.

(*A. Watson, R. Parr*)

5. NUTRITION IN RED GROUSE AND PTARMIGAN

Spring nutrition—field work

An important factor determining the breeding success of red grouse and ptarmigan and possibly the behavioural type of young produced (see p. 15)

is the quality of the eggs laid. This may depend on the quality of the food eaten by the hens laying the eggs. The major nutrients which are in shortest supply in spring heather and which are selected for by the birds are nitrogen and phosphorus. We can therefore use levels of nitrogen and phosphorus as an index of food quality in spring.

We are studying variation in food quality at eight different study areas: two grouse areas on rich soils, four grouse areas on poor soils, and one ptarmigan area on a rich and another on a poor soil. At the ptarmigan areas we are sampling *Empetrum hermaphroditum* and *Vaccinium myrtillus* as well as heather. The hypothesis we are testing is that variations in the nitrogen and/or phosphorus content of the food in spring should parallel variations in breeding success later in the same year. We do not necessarily anticipate that all the variability in breeding success will be accounted for by this measure, because each population is made up of a number of year-classes which we think have different properties and may react differently to a given plane of nutrition. Whether this postulated variation between year-classes is determined entirely by nutrition or whether processes such as genetic selection contribute to it, is a problem which is being tackled by rearing in captivity (see p. 15).

Spring nutrition—work in captivity

We feed our captive stock of red grouse a pelleted diet which, as far as we can tell from knowledge of poultry requirements, contains all known nutrients (including N and P) in excess. As well as the pellets, the birds are given a supplement of a small bunch of heather every day, which forms only a small proportion of their diet. Hens fed freshly-growing heather in three laying seasons laid significantly more eggs at a significantly faster rate than hens fed a supplement of dormant heather cut in winter and stored in deep freeze. The quality of the eggs, as indicated by hatchability and the survival of the young, did not differ between the two groups; and there was no significant difference in the date when the first egg was laid. Some factor that stimulates breeding was apparently present in greater amounts in the freshly-growing heather than in the dormant heather.

The relevance of this to field observations is not yet clear, and the result in captivity may be an artefact of laboratory conditions. On the other hand, these results show that breeding may be stimulated *independently* of levels of major nutrients. This is one possible reason for the well-known selection of newly-growing material by many species of grouse in spring. This is not a unique observation, as stimulation of breeding by something in the early growth of vegetative food has also been noted in lagomorphs, rodents and kangaroos.

Quantity of food available to grouse

Although red grouse only eat a small proportion of the heather available on their territories—usually not more than 5 per cent.—other animals also eat heather and so may compete with the grouse. We are studying grazing by clipping and exclosures on two areas: Corndavon, a phosphorus rich grouse moor partly overlying diorite, where the main grazing animal is the mountain hare (*Lepus timidus*); and Abergeldie, a phosphorus poor moor over granite where red deer are the main grazers.

The main aim is to see whether two correlations, observed from earlier extensive surveys are maintained on individual study areas. The correlations were (*a*) between shoot length one summer ('growth') and breeding success the next season, and (*b*) between winter dieback and the next summer's breeding success. The earlier study was done on 17 study areas over 2–3 years and the correlations were therefore mostly due to differences between areas rather than differences from year to year within areas. So far the new data confirm the fairly low correlation between (i) winter loss of heather (i.e. grazing plus dieback), and (ii) subsequent breeding success ($r \simeq 0{\cdot}4$, using data from Corndavon and Abergeldie). However the relationship is between percentage dieback plus grazing and subsequent breeding, not between amount of material disappearing and breeding. Furthermore, the *amount* of food left in the spring bears no relation to subsequent breeding success—presumably what happens is that percentage dieback plus grazing indicates a deterioration in *quality*. Our present limited data show no relation between production each autumn and breeding success the next year, and thus conflict with the earlier results. Two possible reasons for this may be:

(i) We do not yet have enough data to show a relation, which may yet prove to exist.

(ii) Shoot length (the measure of growth used in the earlier correlations) is not particularly well correlated with actual production (present measure: $r \simeq 0{\cdot}6$, $r^2 \simeq 36\%$). Thus about half to two-thirds of the variation in shoot length is accounted for by factors other than production.

Another hypothesis put forward in 1963 was that cock grouse might adjust their territory sizes to the amount of food available in autumn. This was refuted in 1966 on the ground that shoot length in autumn bore no relation to grouse stocks. Similarly, present results show no relation between heather production and grouse stocks. However, the hypothesis has recently been revived by A. Lance who has shown an inverse relation between territory size and the N content of the heather in individual territories within years. This indicates that the amount of adequate-quality food, as opposed to the gross amount of green heather, is related to territory size. However, my data show that this does not apply on a population basis amongst years i.e. changes in the chemical composition of the heather in autumn between one year and the next bear no relation to changes in grouse stocks.

Production and utilisation of heather

Some other preliminary points are emerging from this work. Two factors—altitude and soil—appear to affect the production of heather independently of annual variation in production. Corndavon, a 'rich' area is rather higher (450 m) than Abergeldie (400 m), a 'poor' area, but usually produces more heather. However Kerloch, another poor moor over granite, at about 180 m altitude, produced more heather than Corndavon in the two years when both were studied.

Annual variations in production of new shoots have been considerable, Corndavon varying from 172–284 g/sq m, Abergeldie from 135–215. Heather at both areas tended to perform in roughly the same way in different years, but this trend was not very precise.

Relatively little heather was usually removed by grazing in summer,

amounting to about 10–15 per cent. of the production. It appeared that the amount of winter grazing was affected by two factors: (*a*) the amount of material available in autumn (i.e. production), and (*b*) dieback. Grazing tended to be high when production was high, but if dieback was also high then grazing was lowered. In some years production was quite good, but negligible grazing occurred because dieback was high. In other years, with a similar level of production, dieback was low and grazing quite high. These relationships can be approximately expressed, from a preliminary analysis, by the following rounded-off equation which fits data from all years at all four areas studied:

$$\text{Grazing} = (0{\cdot}5 \times \text{production}) + (0{\cdot}5 \times \text{dieback}) - 50 \text{ g/sq m}$$

Because production was on average about 200 g/sq m and dieback 50/sq m production was generally about four times as important as dieback (though not in certain years) in determining the utilisation of the available heather.

Digestibility trials

Work on the digestion of heather by red grouse will be published shortly. Results given in the 12th Progress Report of the Grouse Team showed that grouse were capable of digesting about 35 per cent of the cellulose and lignin in heather and about 35–40 per cent of the dry matter. However, more work shows that this ability is facultative and is used only when intake is relatively low (e.g. 50 g dry matter per day). Intake was low in some of the earlier data because the birds were accustomed to a high-energy artificial diet, and did not eat as much heather as birds given a longer period to adjust to the new diet. On fairly high voluntary intakes of about 75 g of dry matter per day, the birds digested only about 25 per cent of the heather's dry matter and relatively little cellulose and lignin.

We are also studying natural foods eaten by ptarmigan, and so far we have done trials with *Polygonum viviparum* bulbils, and *Vaccinium myrtillus* berries. In co-operation with A. Gardarsson and G. Olafsson of Iceland, the *in vivo* digestibility of some foods is being compared with their *in vitro* digestibility using sheep rumen liquor. If the two measures approximate each other, the easily-performed *in vitro* method will be very useful for assessing the nutritive value of a wider range of foods than will be possible using *in vivo* methods.

Food selection in red grouse and ptarmigan

It has already been mentioned that red grouse select their food so as to increase the levels of N and P in their diet. Another point is that as spring approaches a slight change in the birds' diet occurs: heather decreases from almost 100 per cent to about 90 per cent of their diet, and other, freshly-grown foods begin to occur in the crops. In some cases (e.g. *Rumex acetosa*), this boosts the N and P content of the diet but on some areas *Erica tetralix* and *E. cinerea* form a major part of this new material because little else is available. This does not increase the N and P content of the diet. However, the Ericas do grow earlier than Calluna, and we may speculate that the birds are eating this material in order to obtain the nutritional factor discussed above (spring nutrition-work in captivity). Alternatively, nutrients in the freshly-growing foods may be more available to the birds even though the gross amounts are the same.

Ptarmigan in Iceland are better subjects than either red grouse or Scottish ptarmigan for studying some aspects of food selection because they eat a large variety of different foods and show marked preferences. These preferences are being studied by A. Gardarsson, and chemical analyses have been done on a number of foods in an attempt to explain some of the preferences. In short, most of the observed preferences can be understood because the birds are choosing the most nutritious of the available foods. How they do this is another question.

(*R. Moss*)

6. Viability and Behaviour of Young Red Grouse and Ptarmigan

In arctic and subarctic areas, numbers of many species of birds and mammals fluctuate in fairly regular cycles. There is a vast literature, with much speculation but with very few studies based on detailed field observations or experiments throughout a fluctuation.

There is some evidence that decreases in numbers of red grouse and ptarmigan follow the production of year-classes of young of poor 'quality'. This poor quality may result in high mortality of the small chicks, as in Scotland, or in a greater rate of loss of full grown juveniles over the winter, as in Iceland (unpublished work by Dr Finnur Gudmundsson). These findings need to be documented further. Together with field studies to check this point, we are doing an experimental project to give information on the proximate causes of poor breeding in these species. One possibility is that the production of young (in Scotland) in summer, or their survival rate after the summer (Iceland), is affected by factors after the eggs hatch, for instance by bad weather, lack of food, or food of poor nutritive value, which might all weaken or kill the chicks. Alternatively, the survival of the chicks might be predetermined before they hatch, by the quality of the eggs, and in turn by the nutrition, condition and possibly 'quality' of the parents.

There is some evidence for both possibilities in northern game-birds, but the question is still wide open because so little experimental work has been done. Our experiments with red grouse and ptarmigan now show that chick survival is affected much more by pre-hatching influences (egg quality) than by factors after hatching. The experimental evidence is that when eggs are taken from the wild to standard conditions in captivity, the captive chicks survive poorly in years when chicks do badly in the wild, and *vice versa*.

There is also evidence in red grouse (and to some extent Scottish ptarmigan also) that territorial birds reared in years of poor breeding are more aggressive and occupy large territories, thus producing a decline in population. However our understanding of this process is far from complete. We are interested in finding whether the aggression of a bird is already pre-determined before hatching in the same way as its probability of survival.

We take eggs from wild nests and rear the chicks in captivity. The growth rate, survival and aggressive behaviour of the chicks are measured, and compared with population density and breeding success in the wild, and with the production and nutritive value of the food supply.

Over several years, enough populations will be studied to cover the different stages of their fluctuations. The conditions in captivity should eliminate any effects of variable food, weather or other post-hatching influences. If the aggressive behaviour of the different year-classes of grouse

and ptarmigan is different, this will show that pre-hatching factors are important. If it is the same, this will suggest that post-hatching factors cause the observed variations in aggression which occur in the wild. Preliminary results indicate definite differences in aggression between different year-classes in captivity, suggesting that pre-hatching factors do affect aggression. As this project is combined with other work on the quantity and nutritive value of the food in the wild, the research should also provide evidence either confirming or refuting the importance of the parents' spring nutrition for subsequent breeding success and/or aggression.

(R. Moss, A. Watson, R. Parr, R. Hewson, W. Glennie)

7. Red Grouse in Ireland

This is a co-operative project with P. J. O'Hare and the Agricultural Institute at Glenamoy in County Mayo, in the west of Ireland. The main aim is to increase grouse stocks in parts of western Ireland where shooting was once good but where grouse were thought, in 1966, to be nearing extinction. The project is financed by the Game and Wildlife Branch of the Department of Lands in Dublin, and is technically directed by An Foras Taluntais (The Agricultural Institute). As tourism is now a major industry in Ireland and shooting an increasing part of it, grouse are an important natural resource. In some parts of eastern Ireland, near Belfast and Dublin, where the climate is dry and heather predominant, grouse are still fairly common. But they are apparently much scarcer than they used to be, probably for the same reason as in much of eastern Scotland: underburning, with large expanses of rank old heather and hardly any small fires. Even lower stocks in Ireland occur on the vast areas of moorland or bogland in the wetter climate of the west.

Research at Glenamoy on the nutritive requirements and other aspects of the growth of heather is already well advanced. The climate is extreme oceanic with an annual rainfall of 125–140 cm distributed over some 270 days. Blanket peat, approximately 4 m deep, and typical of much of western Ireland, covers a rolling countryside. The peat lies directly on a shallow highly podsolised soil, derived mainly from quartzite. The impermeable nature of the peat prevents any upward movement of nutrients from the underlying soil, and thus the surface vegetation is mainly dependent on nutrients from atmospheric precipitation. The characteristic plants of blanket peat in western Ireland are *Schoenus nigricans* (black bog rush) and *Molinia caerulea* (flying bent) but many other species are present. Calluna, though seldom vigorous or dominant, is frequent as a dwarfed plant, and its annual growth is poor. Much of the ground is heavily grazed by sheep and cattle.

The aim of the research is to find if grouse stocks can be increased by experiments such as draining, fertilising, and fencing to control sheep and cattle. At the same time, observations are being made on the behaviour and natural population regulation of the grouse in an extreme situation where they are at a very low population density. This has necessitated different methods from those used in West Scotland. Fourteen study areas have been used, including one area used for an intensive I.B.P. study of productivity by University College, Dublin, where we provide some data on secondary production of vertebrates.

Grouse numbers are extremely low by Scottish standards, varying from

2 to 5 pairs per km², but there are grouse on every area we have looked at, so they are clearly not in danger of extinction. However, they are so scarce that shooting is not worthwhile. Other wild animals, such as hares and golden plovers (*Pluvialis apricaria*), are also scarce.

Counts with dogs are done in spring to find the size of the breeding stock and in August to measure the birds' breeding success. Behaviour observations involve watching at dawn and dusk. This shows that the grouse sing and show aggressive behaviour and courtship at certain favoured sites. They also meet one another in threat display between these sites, and each cock crows and flies around a small local area where heather is relatively abundant. The activity occurs in twilight, so that the birds are not visible, but this is probably a form of territorial behaviour. Discrepancies between one count and its repeat are cleared up by these dawn observations. Counts with dogs plus behaviour observations are essential complementary methods for finding the exact number of birds resident on these areas.

Grouse breeding stocks have greatly increased following two experimental treatments:

(*a*) drainage and application of phosphorus fertiliser and trace elements to small 2 ha plots scattered here and there on a larger area of open bogland which was all fenced to exclude sheep and cattle, and

(*b*) fencing to exclude sheep and cattle on a well-drained hillside where heather was naturally dominant but was previously heavily overgrazed.

Breeding success has also greatly increased on the drained and fertilised area.

Note—Fuller data on the counts and on the nutrition of heather are given in the Progress Reports on Red Grouse, by P. J. O'Hare, Agricultural Institute, Oakpark, Carlow, Ireland.

(*A. Watson, R. Parr*)

8. Telemetry Studies of Red Grouse

From 1968 until early 1971 I have been concerned with ways of testing some of the conclusions from the Grouse Team's previous research into the population processes of red grouse. The relationship between nutrition and behaviour has been my main interest, with much of the data obtained by radio telemetry.

My work has tested two main ideas: (*a*) that the success or failure of young grouse in gaining territories is affected by the nutrition of their parents, and (*b*) that the size of territory occupied is adjusted to the nutritive quality of the main food, heather, occurring within that territory.

Information on the first topic was sought from intensive investigation of the daily and seasonal activities of selected individual breeding birds and their offspring. The aim was to try and predict whether certain young grouse selected for study became territory holders or surplus non-territorial birds. The basis for the attempted predictions was information on the characteristics of the parents, and on the chicks' own upbringing. The history of some radio-marked birds has been obtained from before their birth until nearly two years of life afterwards. In order to achieve this, the individuals were recaptured periodically and new transmitters fitted.

The extensive work involved estimation of the nutrient resources of territories by several criteria, and comparison of these estimates with territory

size. Since changes in territory size reflect changes in the size of breeding populations, heather quality could be a direct link between the two.

Preliminary analyses of the data suggest that the ownership of at least some sections of heather moorland is inherited through successive generations. Young males compete, brother against brother and son against father, for their father's territory and ground adjacent to it. Some fathers have moved aside, and others have been evicted altogether. Thus it seems that, among males at least, the annual competition for territories and the right to breed are largely a family affair. So far, however, the role of females in this process is unknown, and the demographic and genetic consequences are still to be investigated.

Territory sizes are inversely related to the mean percentage of nitrogen, which is assumed to be an index of the nutritive value of the heather within them. If grouse adjust the size of their territories to compensate for poor heather, differences in total nutrient reserves from one territory to another become reduced. Variations in heather quality account for between one third and one half of the variability in territory size, and previous work by A. Watson has shown that a similar amount of variation in territory size is related to aggressive behaviour. Hence, as with the relationship of cover or visibility to territory size, heather quality may exert its effects on territory size by influencing aggressive behaviour.

By depending heavily on telemetry for its success, the intensive work on young grouse has provided an opportunity to evaluate the suitability of this widely-heralded technique in research for which it is ideally designed, and for its effects on the birds themselves. Telemetry has subtle though recognisable effects on the speed of flight in some red grouse, which may place such birds at greater risk of predation. The evidence for heavier predation is slight, however. There are also slight indications of an effect on the breeding of the hens. Adult males appear to be least affected, which is consistent with the idea that the problem is mainly one of weight. Red grouse may be at the threshold of size and weight for a species of their temperament to carry 25 g transmitters without effect. Despite these limitations, telemetry used with discretion can still provide access to problems difficult to tackle by any other means.

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

9. The Effect of Radio Transmitters, carried by Red Grouse, on their Biology

Radio telemetry enables ecologists to locate animals from a distance and thus to measure movement and home range. It has eliminated the possible effect of a human observer on the animal. However, the radio might influence the animal's behaviour. This possibility was investigated using penned and wild red grouse from 1970–71, when I visited the Grouse Team during my sabbatical year. Measurements were made on activity, food consumption, and choice of position within the pens. Two other attributes were studied in wild red grouse; their survival rate and their success in entering the breeding population. The question asked for each attribute was: does the equipping of grouse with the radio transmitters cause a significant change in the bird's behaviour?

To study the effect of radio transmitters on penned grouse, 20 captive-reared birds aged 10 to 16 weeks were divided randomly into a control group

(six males and four females) and an experimental group (seven males and three females). All 20 birds were housed in contiguous pens, each containing four different 'habitat' types varying in cover and other features, and a treadle for recording their activity electronically. The attributes being investigated were measured in all 20 grouse for 18 days (18 September–6 October) prior to equipping grouse in the experimental group with radio packages. All were then measured for an additional 18 days (8–25 October). This programme allowed me to compare the behaviour of the two different groups and of the two sexes both before and after radios were put on grouse in the experimental group.

To investigate the effects of radio packages on free-ranging wild grouse, a sample of 40 immature birds was caught in October (20 males and 20 females). Ten males and ten females were equipped with dummy radio transmitters and batteries, and then released. The remaining 20 grouse were back-tagged and released, using the Grouse Team's standard methods for marking wild grouse. The fate of these 40 birds is being followed until the summer of 1971.

Results from the study of grouse held in pens have shown the following:

(*a*) Activity of grouse carrying radio packages was significantly depressed, most markedly in the first week after the radios were put on.

(*b*) Food intake among males wearing radios was not significantly affected, but that of females was significantly reduced.

(*c*) Choice of 'habitat' in the pens was not significantly influenced among grouse wearing radios. However, there was a suggestion that females with radios avoided areas with overhead cover.

It is too early yet to give results from the study of wild grouse.

(*D. A. Boag, Senior Visitor from University of Alberta*)

10. Development and Aggressive Behaviour in the Red Grouse in Captivity

This three-year study, which is now completed, has been an attempt to gain a better understanding of the factors involved in variation in aggressive behaviour and clutch characters in the red grouse.

Variation in physical clutch characters (egg weight, hatch weight, growth rate and chick survival to 14 days) and in chick behaviour (frequencies of activity and distress cheeping) are described for clutches and for groups of chicks of different origins and from different year-classes. Analysis of the relationships between these clutch characters showed few overall correlations and thus did not indicate a small number of unitary causative factors behind the variation. The only general correlations were between survival and early growth rate, and between cheeping frequency and growth in the second week after hatch.

Comparison of hens breeding in captivity showed that good chick survival resulted from a heavy hen parent. One-year-old hens produced faster-growing chicks than two-year-olds. A study of breeding over one generation showed that egg weight, hatch weight and growth to four days showed varying degrees of maternal inheritance, but no indication that genetic inheritance affected these characters to any significant degree.

Observation on groups of chicks from hatch to maturity showed no organised social structure based on aggressive behaviour that might have a

direct influence on the dominance interactions of adults. However, chicks in one small group could be ranked on avoidance of each other.

The dominance of adult cocks in captivity was measured in small, temporary groups, and a dominance index was calculated for each bird relative to the others in its group. The rankings so obtained were stable for at least a year when the same birds were retested, provided that a fair amount of aggressive interaction took place and a range of aggressive types was present. Methods of pair testing and isolation testing were developed and compared with group rankings. Both were discarded because they failed to produce consistent aggressive reactions in birds.

Dominance was negatively correlated with late juvenile growth, and positively correlated with comb size which is an indicator of testosterone activity. More dominant birds also tended to be older, and moulted their primary feathers earlier. A model for the development of aggressive behaviour is proposed in my thesis: external influences depress growth, thereby accelerating moult and increasing androgen production, which in turn determines adult dominance through aggression. This is discussed in relation to the model of population limitation by territorial behaviour in the red grouse.

(H. Kolb, Ph.D. Student)

11. The Feeding Ecology of Red Grouse in N.E. Scotland

This study, now in its third and final year, involved measuring the food intake of red grouse, and studying factors controlling the quantity and quality of food intake. Most field work was done on two neighbouring Kincardineshire moors, Spyhill and Kerloch, backed up by experimental work on the captive grouse at Blackhall. The aim was to see how annual and seasonal food requirements of grouse are related to territory size, heather quality, breeding success and fluctuations in population density, between years and between moors lying over rock of different base-richness.

I estimated the food intake of wild grouse at Spyhill by regularly measuring their pecking rates for each hour from dawn until dusk (when feeding ceases), and calculating the total daily number of pecks on a monthly basis. Some grouse were shot each month on Kerloch and the average size of heather particles ingested was calculated from the material in the crop. The daily intake of heather (g dry weight) can then be estimated for each month and for the whole year. Crop contents also show variations in the composition of the diet. Except in June, July and August, heather (*Calluna vulgaris*) forms at least 90 per cent. (by dry weight) of the diet. During these months, the flowers, seeds and leaves of many flowering plants as well as ferns and mosses are also taken, and the proportion of heather drops to 60–80 per cent. The only other food items occurring frequently are blaeberry (*Vaccinium myrtillus*), cross-leaved heath and bell heather (*E. tetralix* and *E. cinerea*) and sheep sorrel (*Rumex acetosella*), loose oats in stubble fields also being important in autumn. I also measured food intake more accurately in captive grouse, by feeding them weighed amounts of grouse pellets. Their diurnal feeding rhythms, as well as their monthly variations in food intake, parallel those of the wild birds very closely, and I measured the effects of activity, air temperature, moult and egg production on food intake more accurately than is possible in the field. During June, July and August the secretive behaviour of wild grouse, when they have growing chicks and are in their

main annual moult, makes field observation practically impossible, so the data from captive birds are particularly important at this time.

I also observed the feeding habits of incubating hen grouse. Their daily food intake is much reduced over this period, and they use up fat reserves accumulated during April and early May. The cock's intake is also reduced, but to a lesser extent. After hatching, broods of different ages were killed and samples were taken of available insects in the immediate area of capture. Study of crop contents shows that the greatest selection for insects (mainly Diptera and Lepidoptera larvae) occurs when the chicks are 5–10 days old, but that they eat far less insects than partridge and pheasant chicks, and are capable of taking in a mainly-heather diet immediately. Also, where moss capsules are abundant, these are highly selected. These observations were made on Kerloch in the summers of 1969 and 1970, when the breeding success of red grouse there was very good. Hence, a high-insect diet is not a necessary condition for good chick survival.

The nutrient content of heather decreases rapidly as the plants grow older, reaching a fairly stable level after 5–6 years, and it also varies between plants of the same age and between parts of the same plant. Grouse therefore have a wide qualitative range from which to select more nutrients. At Spyhill, I collected dung regularly from plots and measured the amount of time spent by grouse on different ages of heather. The data show that they prefer heather aged 4–6 years (18–30 cm in height). On younger and lower heather, birds are more exposed to weather and perhaps to predators, whereas the height of heather older than six years would impede their field of view. However, measurement of grazing pressures (from average peck rates and time spent) shows that three- and four-year-old heather are preferred. Where three-year-old heather is present, grouse tend to move on to this near dusk for their evening peak of feeding. This selection for different heather ages has been tested with captive birds, and early results suggest that the selection shown by grouse depends on their physiological demands and body condition, as well as on the quality of heather offered. When offered one-, two-, three-, five- and ten-year-old heather, cocks in poor condition and hens on point of lay selected young heather, whereas grouse in good condition preferred older heather.

I followed up the earlier work of R. Moss and measured selection from the plants themselves by comparing the nutrient content of the crop contents from shot grouse with that of heather samples taken from where these birds were feeding. These comparisons confirm his results on selection for N and/or P.

(C. J. Savory, Ph.D. Student)

12. Nutrition and Behaviour of Captive Red Grouse

A working hypothesis of the Grouse Team is that the nutrition of the hen prior to laying is a major factor determining her breeding success and the relative aggression of her offspring. Application of fertiliser to the moor in spring, however, has produced on separate occasions both delayed and immediate responses in grouse density. This suggests that there may be post-hatching nutritional effects on the birds' aggression and hence on territory size and population density.

My work, which began in October 1970, is intended to test the null hypothesis that variation in the post-hatching environment has no effect on the

final dominance of a bird, i.e. that it is predetermined in the egg. Two major experiments are proposed, testing the effects of differing (*a*) nutritional and (*b*) social environments on captive grouse chicks. Each experiment involves selecting two batches of eggs from captive birds, so that each batch contains a similar variety of genetic contents and/or 'egg qualities'. The incubation of both batches will be uniform in an attempt to equalise the pre-hatching environment of the embryos.

In the first year one batch of chicks will be fed on a normal diet and the other on a low plane of nutrition. The growth rate and behavioural development of both batches will be measured, and dominance testing carried out in the autumn and subsequent spring, to measure the relative aggression of each bird.

At present (winter 1970/71) my work with captive birds involves developing methods to determine which cocks are preferred and to which characters hens are specifically attracted. The Grouse Team has found that in years of decline many territorial cocks remain unmated despite the presence of single hens and it is possible that these cocks are particularly unattractive. The choice of the hen may be affected by (*a*) the cock's behaviour, (*b*) interaction between hens, and (*c*) the hen's own attraction to a cock. All three factors may be influenced by the relative aggression of birds. I hope to continue this work next winter using birds reared on low and high planes of nutrition, to see if this has an effect on choice by the hen.

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

13. Mountain Hares

Data on populations of mountain hares on all the grouse study areas were analysed recently. On grouse moors in north-east Scotland, there were marked differences in the mean abundance of hares on areas over base-rich, intermediate and base-poor rocks. Hares thus show similar differences in abundance to red grouse and ptarmigan, in relation to the underlying rock. In western Scotland and at high altitudes on ptarmigan ground, hares were on average much scarcer. On the ptarmigan ground they were more common over base-rich rocks than over base-poor rocks.

Fluctuations in the numbers of hares occurred from year to year within areas on all the grouse moors studied. These fluctuations were not in phase on neighbouring moors. They were also not in phase with fluctuations of red grouse on the same area.

Methods were successfully developed for keeping mountain hares in captivity, so it is now feasible to consider feeding trials for measuring food selection.

(*A. Watson, R. Hewson*)

14. Movements and Home Range in the Black Grouse

Introduction

This study obtained information on the home range and mobility of black grouse (*Lyrurus tetrix*), and the social structure of a population. The study was made during 1967–68 on Glen Dye Estate in Kincardineshire during a visit to the Grouse Team in my sabbatical year.

Results

Seven blackcocks (six adults and one juvenile) were equipped with radio transmitters, and a total of 906 locations were plotted.

The size of home ranges varied from 303–689 ha, with an average of 478. The area of concentrated use varied from 48–151 ha. On average, the area of concentrated use was approximately 20 per cent. of the home range of each bird. Only minor changes occurred in the sizes of the home ranges during the different months of this study.

The mean distance between consecutive locations of the same individual was about 300–400 m in all birds except the juvenile bird, which had 517 m, approximately 57 per cent. greater than that of the six adult birds tracked.

By having two to four birds with transmitters in the population at all times, it was possible to study flocking and the stability of groups. The birds were gregarious throughout the study but the groups were not stable in autumn and winter, when birds with transmitters moved freely from one group to another. The stability of the groups increased in the spring, and there were two separate flocks on the study area from April to June. One flock consisted of birds that regularly visited the lekking areas, while the second flock was composed of birds which seldom visited a lek. The lekking flock was composed of 12 to 16 blackcocks; and the non-lekking flock, which was much more mobile, consisted of 19 to 24 blackcocks (both adults and juveniles).

Radio transmitters were also put on nesting greyhens and a detailed record was made of their activities during incubation. The hens with transmitters left their nests to feed regularly at the same time each evening. After hatching, the greyhens made remarkably long journeys with their broods in the first day or two. Habitat use and movements were studied, and the survival of the young was very good in the first few weeks. This exploratory study showed that telemetry did not adversely affect the birds' breeding activities, and that it is a successful method for getting detailed basic information which is extremely difficult if not impossible to get by ordinary human observation.

The tentative results of this study pose several questions for biologists interested in the population dynamics of lekking birds. For instance: what changes occur in the size of the non-lekking group when the total population of blackcocks increases or decreases? Do birds in the non-lekking flock fill vacancies at the lek? Does the more mobile non-lekking group in a densely-populated area supply birds to less-densely populated areas nearby? Is mortality the same among birds in the two different flocks? Does the non-lekking group contribute to the gene pool? Are the results about lekking and non-lekking flocks, obtained in this study, also representative of other lekking groups, e.g. capercaillie (*Tetrao urogallus*), sage grouse (*Centrocercus urophasianus*), or prairie chickens (*Tympanuchus* spp.)?

(*R. J. Robel, Senior Visitor from Kansas State University*)

15. Human Impact on Animal Populations in the Cairngorms

Note—This extract is taken, by permission of IUCN Publications, from the zoological parts of the paper by A. Watson, N. G. Bayfield & S. M. Moyes (1970), IUCN Publns New Ser. No. 16 (Ref. 'Tundra Proceedings').

The construction of new ski-lifts and roads in the Cairngorms region in the early 1960's, and consequent heavy human traffic in summer and winter, have been followed by soil erosion, damage to vegetation and a threat to wild animals on two areas of arctic-alpine ground.

Unfortunately, some of the best areas in Scotland for snow and skiing are

also of great conservation value. Their scientific interest is considerable, as they contain the largest block of mountain tundra in Britain and a corresponding assembly of arctic-alpine vegetation and arctic animals such as ptarmigan, snow bunting (*Plectrophenax nivalis*) and various arctic insects. The Cairngorms mountain massif also contains one of the largest wilderness areas left in Britain and so is of great value to those who appreciate wilderness. Some of the area affected by new or proposed developments lies within or near the Cairngorms National Nature Reserve which is the largest of the Nature Conservancy's Reserves in Britain. The whole region, including much ground outside the Reserve, was one of several Scottish areas chosen as potential National Parks in the late 1940's, though legislation on this was never implemented. There is also a potential threat to animals which are of great interest to tourist naturalists, either (*a*) directly due to human disturbance or (*b*) indirectly due to habitat damage.

Research organisation

A. Watson studied bird populations near ski-lifts from 1962, and in 1966 began exploratory work on the other problems. The first full-time workers were employed by the Nature Conservancy in late 1967; N. G. Bayfield began detailed research on vegetation, soils and people, assisted by S. M. Moyes. A. Mather of the Geography Department at the University of Aberdeen, surveyed the geomorphological problems in 1967–68 and R. C. Welch of the Nature Conservancy's Monks Wood Experimental Station began research on insect populations in 1968.

We decided at the beginning to concentrate on quantitative work on small local areas, if possible experimental, and to leave sociological problems, such as why people come and what they want, entirely to geographers and others who have since begun to study these aspects.

Animal populations

The main approach here was to compare populations on disturbed areas at the skiing grounds and on other nearby areas where few or no people go. At the beginning, the little evidence available (based on anecdotal impressions from a great many people, including scientists as well as local resident gamekeepers and naturalists), suggested that populations would decrease.

Populations of red grouse and ptarmigan were studied at two ski grounds, one at Cairnwell over base-rich schists and limestones and the other at Cairngorm over base-poor granite, with, in each case, appropriate undisturbed 'controls' over similar rocks nearby. Such control areas are essential. Without them, a short-term decrease on a disturbed area over a few years of research might be wrongly attributed to disturbance, yet a decrease might be occurring on undisturbed areas also. Work began at Cairnwell in 1962 and at Cairngorm in 1966. On all areas, the reproductive performance (number of young reared per adult) and the density of the breeding stock of both species have fluctuated from one year to another. However, the critical point is that both species reared as many young and maintained as high breeding stocks on a disturbed area as on the appropriate nearby undisturbed area. On the base-rich areas, both species consistently reared more young (1·4–2·0 young reared per old bird) and also maintained higher breeding stocks (one pair per 1·2–3·0 ha, or one pair per 3–8 acres) than on the base-poor areas at Cairn-

gorm (only 0–0·4 young reared per old bird and breeding stocks dropping to five times as low as the lowest at Cairnwell) and this difference was maintained throughout the period of increasing human use of both areas. It is associated with better nutritive value of the food plants on the base-rich ground.

Studies of behaviour show that even the most disturbed ground is occupied by territorial ptarmigan and red grouse. The birds have become tame and used to people, and pay little or no attention to people passing overhead on the chairlifts or skiing downhill near them. We found two nests within 10 m of a ski pylon, one of them within 3 m of it. Although there is more bare ground on the disturbed areas than on the undisturbed, and thus less vegetation, this difference has not yet gone to a point where the ptarmigan populations have been affected. Likewise the populations of meadow pipits (*Anthus pratensis*) have not been affected on disturbed areas.

Dotterel (*Eudromias morinellus*) populations are very sparse, and even before the ski developments no dotterel actually used the skiing grounds, which are not suitable habitat—the dotterel breeds on flat or gently rolling high plateaux on the tops of the hills, not on the steep slopes. Because of this, we had to take a different approach, studying a population near the skiing ground at Cairngorm but not actually on it. However, this dotterel area is crossed by many walkers in summer, moving out from the nearby chairlift. We compared this with a population on another hill 10 km away where few or no people go. Both areas lie over the same base-poor granite. A third population was studied over a base-rich rock.

The breeding stocks and reproductive performance of all populations of dotterel have gone up and down from one year to another. But in any one year since 1966, the disturbed and undisturbed populations have shown no appreciable difference. Statements, such as that dotterel have decreased in the Cairngorms due to increased human use of these hills, must therefore be seriously questioned, particularly as they were not backed up by any quantitative data. They can also be questioned by D. Nethersole-Thompson's conclusion from a detailed study of dotterel, that reproductive success and breeding stocks fluctuated from year to year, even in decades before large numbers of people came to these hills. Nethersole-Thompson's work was mainly done on the granite hills of the Cairngorms. On the undisturbed third area, over a base-rich schist, we have found that breeding stocks were apparently no higher than on disturbed or undisturbed areas over the granite. However, they consistently reproduced better, rearing 0·7–1·3 young per old bird in different years, compared with only 0·2–0·4 over the granite. Nethersole-Thompson never found it better than 0·4 on the granite, over a longer period of years. These results show similar differences in reproductive success to those shown by red grouse and ptarmigan on base-rich and base-poor areas. It is interesting that an insectivorous bird should show the same trends, suggesting either a difference in the abundance or availability of the invertebrates, or a difference in their nutritive value. These differences in dotterel population dynamics may well be important in relation to human impact, as the base-rich dotterel areas may be threatened by future skiing developments.

The research on insect populations by R. C. Welch was done in 1968 and 1969. The work involved sampling with pitfall traps at a remote, relatively undisturbed site at about 1,200 m on the Ben MacDhui plateau 5 km south of Cairngorm, and at another heavily-disturbed site at about the same

altitude beside the path from the top chairlift station to the summit of Cairngorm. S. M. Moyes did the sampling about every two weeks from the main thaw (usually late June) until October. It was very much an exploratory piece of work, as so little background information was available. In fact it was the first time that insects have been sampled throughout a whole spring-autumn season at the same sites on the arctic-alpine zone in Scotland. Previous visitors have collected only sporadically, but we do now have the possibility of finding within-season changes in the abundance of different species as well as of looking for evidence of differences due to disturbance of vegetation and soils as a result of human impact.

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

Range Ecology Research Group

I. A. Nicholson

1. Introduction

Extensive tracts of unfenced land supporting natural or semi-natural vegetation, which is grazed by wild or domestic animals, are often called 'range'. This type of land, usually characterised by low productivity, lies beyond the boundaries of control by intensive agriculture. Although the term range is adopted in many parts of the world it has not generally been applied to the British uplands. This may reflect the tendency to consider our mountains and moorlands in a fragmentary way from the standpoint of different economic uses, e.g. sheep farming, forestry, red deer and red grouse management. To a large extent these uses have been regarded as mutually exclusive, thus making it difficult to take a comprehensive view of the uplands as a distinct type of land resource.

This area of mountains and moorlands extends to 6·8 million ha in the whole of Britain, with 4·8 million ha in Scotland where it represents two thirds of the land surface. In Scotland, National Nature Reserves cover a total of 74,000 ha of which 75 per cent. comprises range-type land, and range is well represented in upland reserves in other parts of the country. Accordingly, the programme of the Range Ecology Group has developed in close consultation with the members of the Mountains and Moorlands Habitat Team.

This report summarises progress in the main lines of work in range ecology. The Range Ecology Group was established in 1968 from two units which were formerly engaged separately in botanical and zoological research. The aim has been to combine different disciplines in a single team to foster, under range conditions, the study of relationships among soils, plants and grazing animals, and between the major land uses and wildlife (Research Programme and Planning Papers, 1969). The Group is not specifically concerned with woodland problems or the ecology of birds which are the responsibilities of other groups.

The research aims in range ecology are: to investigate the factors maintaining the present status of upland vegetation and animal populations and to determine the capacity for vegetational change on various types of sites; to study the interrelationships between vegetation and different animal populations, and the ecological implications of recreation. At this stage in implementing the programme these aims are being emphasised but, in due course, it is proposed to study the synthesis of alternative systems of management and patterns of land use in relation to ways of optimising nature conservation.

Twelve separate research reports and an account of the development work on Glenfeshie estate are described here. The various projects are at different stages, hence some accounts give more data than others.

Part of the research is being done on National Nature Reserves including the Island of Rhum, Inverpolly, Craigellachie and the Cairngorms National Nature Reserve. Study areas elsewhere are also being used where conditions occur that are particularly suitable for research, e.g. at Glenfeshie, which contains a section of the Cairngorms reserve, birch regeneration is being studied together with certain aspects of red deer ecology.

At present there is an emphasis on red deer and associated problems in the deer/range system, with the immediate objective of improving the capability for deer management and for achieving desired trends in habitat. The emphasis on red deer arose partly from historical reasons, as research on this animal had begun ten years before the group was set up, and partly from a growing demand that this research should be intensified. The Conservancy had also developed a close relationship with the Red Deer Commission, and an agreement had been entered into between the Nature Conservancy and The West Highland Woodlands involving a commitment in the management and development of Glenfeshie estate (Glenfeshie: Progress Report 1966–69). For these reasons most of the group's research has been concerned with problems in the forest zone. The red deer and the land management that goes with it is a major factor affecting the natural flora and fauna on an area of 2·8 million ha. Thus an understanding of the ecology of red deer and their effects on nature conservation and other land uses involves questions of considerable importance both on reserves and in the countryside in general. Much of the botanical work is related to problems of plant establishment, vegetational succession and site potential, and is therefore concerned with broader issues than plant/animal relationships or the habitat of red deer in particular. None of the main projects deals with the ecology of the montane zone, except indirectly through the study of recreation and red deer, but it is hoped to intensify work in this field as soon as resources allow.

Many problems in the mountains and moorlands will arise from the changing pattern of land use in response to changes in economics, government policy and the increasing demand for recreation. Some changes may affect nature reserves directly, while others will have an indirect influence through their impact on adjoining areas in economic use. The Conservancy's programme in range ecology is aimed at increasing our capability for managing wildlife on reserves. It is also designed to link with the research of various bodies whose aims relate to other uses. These uses and the new relationships that develop among them may bring further conflicts with wildlife conservation. Equally, new opportunities may arise as a result of changes which will present challenging problems for ecological research.

2. Consequences of Species Poverty in the Uplands

Floristic poverty is a common characteristic of upland vegetation. Destruction of the original woodland cover has been taking place since Neolithic times and is now almost complete. The most frequent and extensive kinds of vegetation now existing in place of woodland usually contain few species of flowering plant. Commonly, they also show a certain inertia or resistance to successional change because of soil and ground surface conditions that are unfavourable to plant establishment. These have resulted from the effects of past management and of the dominant species themselves. Thus when management is altered the species composition of the vegetation may change negligibly over a long period.

Several consequences follow from these characteristics of upland range. Desired species, especially sward formers and trees and shrubs, are frequently lacking, and therefore must be introduced. However, establishment is difficult and uncertain. Although techniques have been developed by agriculturists and foresters for establishing both groups, they are inapplicable

in many circumstances because of cost. There is thus a need for further information on ways of establishing plants by direct seeding. It is also difficult to assess the potential of a site for supporting different species and vegetation. Any site can support a variety of species and vegetation types under different kinds of management, but selection of the best types for any given range system requires a knowledge of the possible alternatives. Another consequence is that the secondary successions undergone by vegetation following disruption are abbreviated, so that there may be few if any significant changes that can be achieved in practice by attempting to initiate and control succession. Thus, a current study of recolonisation after soil was bared at three different heather moor (Callunetum) sites shows that at all sites recolonisation is tending directly to regenerate the original vegetation.

These consequences have stimulated this work. The aims are (*a*) to determine what alternative species and vegetation types can be supported at different sites; (*b*) to study problems of plant establishment, with particular reference to trees and shrubs, emphasising the effects of surface conditions on germination and early seedling life.

An initial experiment was designed to give information about alternative species and vegetation that could be supported at four sites in north east Scotland. Three sites bore Callunetum: Glendye with an iron-humus podsol, Glensaugh with a peaty podsol, and Deskry with a brown forest soil. The fourth site, also at Deskry, was on reclaimed grassland. Seed of 111 species was sown on bared soil as six mixtures, five based broadly on life form (short perennial herbs, tall perennial herbs, herbaceous weeds, ruderals and pioneer species, small shrubs (excluding ericoids) and trees while a sixth comprised species characteristic of Callunetum.

It has been found that all sites can support more species, and hence potentially more vegetation types, than at present. Most species responded similarly at each site, using performance at the grassland site as the standard. The sites could be ranked in the same order by the numbers of species establishing (Table 1) and by the establishment success and vigour of individual species: Deskry (Grassland)>Deskry (Callunetum)>Glendye>Glensaugh. This suggests it is feasible to use individual species as indicators. However, although the direction of response by most species was the same, the degree of response varied widely. Additions of fertiliser greatly increased establishment.

TABLE 1. Number of species present at each site after one and two growing seasons (latter in parentheses)

	Glensaugh	*Glendye*	*Deskry (Callunetum)*	*Deskry (grassland)*
Unfertilised	40 (34)	64 (65)	75 (74)	79 (82)
Fertilised	88	87	79	64

A number of species appear promising as indicators of site potential, including common bent-grass *Agrostis tenuis*, heather *Calluna vulgaris*, hemp-nettle *Galeopsis speciosa*, Yorkshire fog *Holcus lanatus* and greater woodrush *Luzula sylvatica*.

High mortality rates of seedlings are a feature of natural establishment. Current studies seek to identify the causes of death so that their effects may

be lessened and establishment ameliorated. A survey on part of Glenfeshie estate of seedlings self-sown on soil bared by natural causes showed that 82 per cent. of the current year's seedlings present in autumn 1969 disappeared over winter. Fewer than 1 per cent. were present as dead plants in the spring. It is possible that many of these vanished seedlings were uprooted by frost heaving of the soil. Most were very small and could easily have been washed away afterwards. Frost heaving certainly caused the death of up to 40 per cent. of tree seedlings in the establishment experiment described earlier.

One way of obtaining information about the requirements of different species for establishment is by experimental interference in the field. Thus the effects on establishment of different sizes of openings in the vegetation are being studied on a species-rich moor. Several species, including heath bedstraw *Galium saxatile*, tormentil *Potentilla erecta* and common violet *Viola riviniana*, established most abundantly in small (25 cm^2) openings, whereas broom *Sarothamnus scoparius*, established best in large (2,500 cm^2) openings, and hardly at all in small ones. Differences of this order obviously have practical implications.

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

3. Effects of Herbivores on Range Vegetation Types

Work began in 1969 to quantify the relationships between herbivore numbers and botanical composition in several important moorland vegetation types. With this information the effects on vegetation of grazing regimes can be predicted, and vegetation can be manipulated in specified ways by means of the grazing animal.

The overall approach is to measure herbivore usage at a number of diverse sites, record their effects on vegetation over a four-year period, and obtain a general relationship by interpolation. The 32 sites selected cover a wide range of altitude and soil conditions, but the arctic-alpine zone above 700 m and blanket peat have been avoided. The sites were chosen to include a considerable number that are likely to show succession if the present intensity of free-range grazing continues. Red deer, cattle, sheep and mountain hares are the chief herbivores, and sites predominantly grazed by each have been obtained, although mostly mixed grazing occurs.

Animal numbers are assessed by the dung-volume method; a subsidiary project is the testing of this method and the derivation of conversion factors for the dung of different herbivores. At each site, dung deposited on plots totalling 120 m^2 is measured at three-weekly intervals, using water displacement. Measurement of botanical composition takes place alongside the dung plots every second year, using 800 point quadrats per site in permanent positions and taking standing crops from eight 2 m$\times$0·5 m plots. Measurements are also made in permanent plots of *Calluna* height and growth at the end of each growing season, and the degree of recent grazing on the main species present is assessed four times a year.

Results cannot be reported until the measurements of botanical composition have been repeated in summer 1971. It is already clear, however, that at some sites grazing pressures have been sufficiently light to allow succession towards dwarf-shrub heath to proceed, whilst at other sites ericaceous species have been depressed and succession towards graminaceous vegetation is occurring. At certain heavily utilised sites, *Nardus* has been

severely grazed, suggesting that it is intermediate grazing pressures, not heavy, that encourage its spread. *(D. Welch, T. Parish, E. Kemp)*

4. Birch Regeneration in Relation to Site Characteristics

Birch is the commonest natural woodland type remaining in the Scottish Highlands. It gives shelter and provides browse for animals. Some birchwoods are vigorous and contain an abundance of young trees, but most are moribund because of a failure to regenerate. Conditions associated with good and poor regeneration were identified by studying the distribution and abundance of young birch at 20 diverse woodland sites in the western, central and eastern Highlands. Although comparatively abundant, few seedlings appeared to survive as saplings to the second year (Fig. 1). No saplings older than 10 years were found in grassland, and in heather communities none older than 31 years occurred.

Most variation in seedling density was probably due to the nature of the seed bed. The most favourable surfaces for establishment, bare soil and patches of 'compact' Sphagnum, were scarce. They accounted for only 4 per cent. of the total area surveyed and yet carried 50 per cent. of all seedlings counted. The extent of the canopy provided by trees, dwarf shrubs and ferns did not affect the number of seedlings, and grazing was not of direct importance. However, trampling by large herbivores may create niches for seedling establishment by disturbing moss and litter and exposing bare soil.

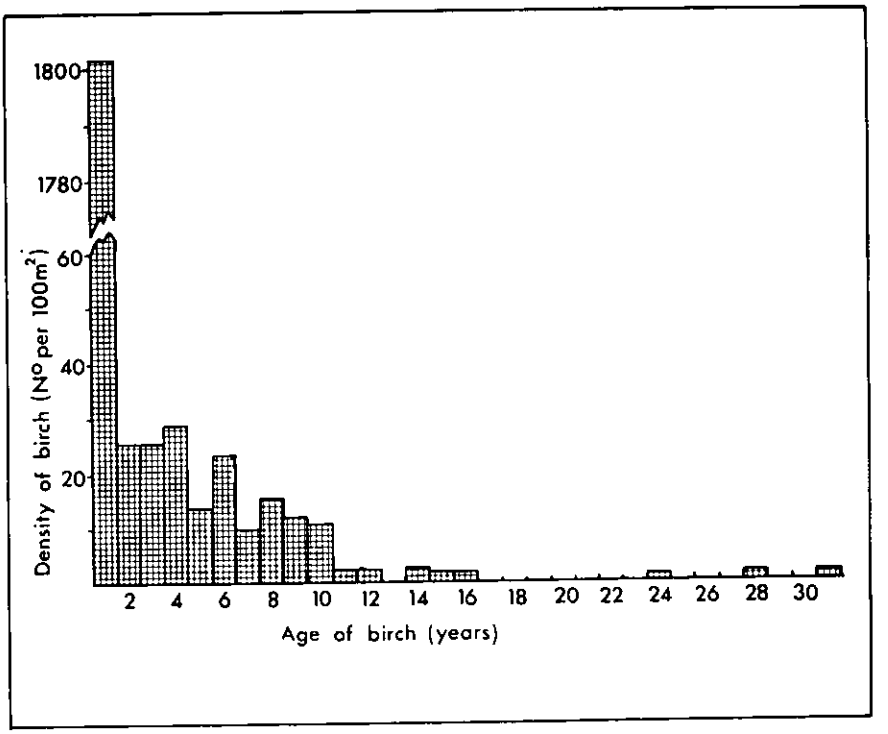


Fig. 1—Age structure of young birch population (mean derived from 20 sites).

Sapling density was related to the presence or absence of a canopy, and to grazing. Saplings were sparser and smaller under dense woodland canopies than on open ground. By contrast, at *Calluna* sites, sapling density increased with the amount of heather canopy. Under these conditions the heather appeared to protect the saplings from grazing until they emerged above the canopy. At grassland sites, the density and height of birch saplings decreased as grazing pressure increased.

(*J. W. Kinnaird*)

5. Effect of Shade on the Growth of Birch

The field survey indicated that the scarcity of young birch in mature birchwoods might be due to a combination of grazing, shading and root competition. This suggested experimental work and initially a study was made of the effect of shade on the growth of birch seedlings. Two species, *Betula pubescens* and *B. pendula*, were compared. *B. pubescens* had a uniformly lower relative growth rate than *B. pendula* at all levels of shade (Fig. 2). In the shade treatments, measurements gave mean relative light intensities of 16, 28 and 56 per cent. compared with the maximum experimental light levels

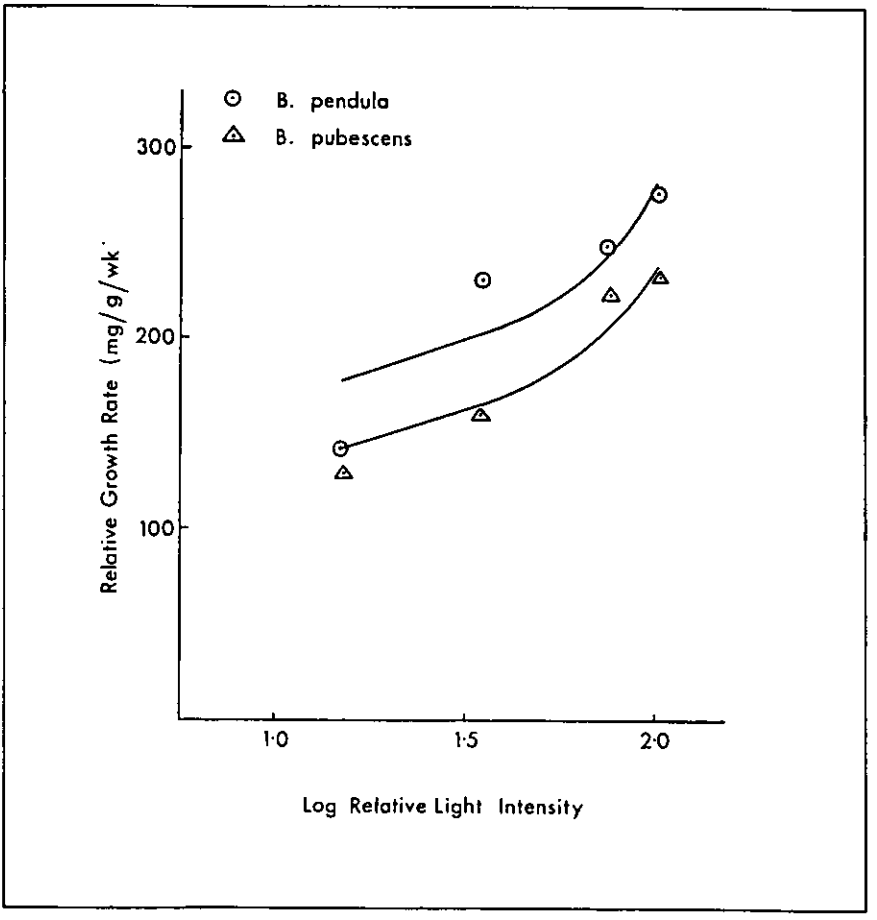


Fig. 2—The effect of shade on the growth of birch.

in the control treatment in which shade was minimal. The fall-off in the growth rate of both species with increased shade suggests that shading contributes to the sparsity of birch regeneration in birchwoods.

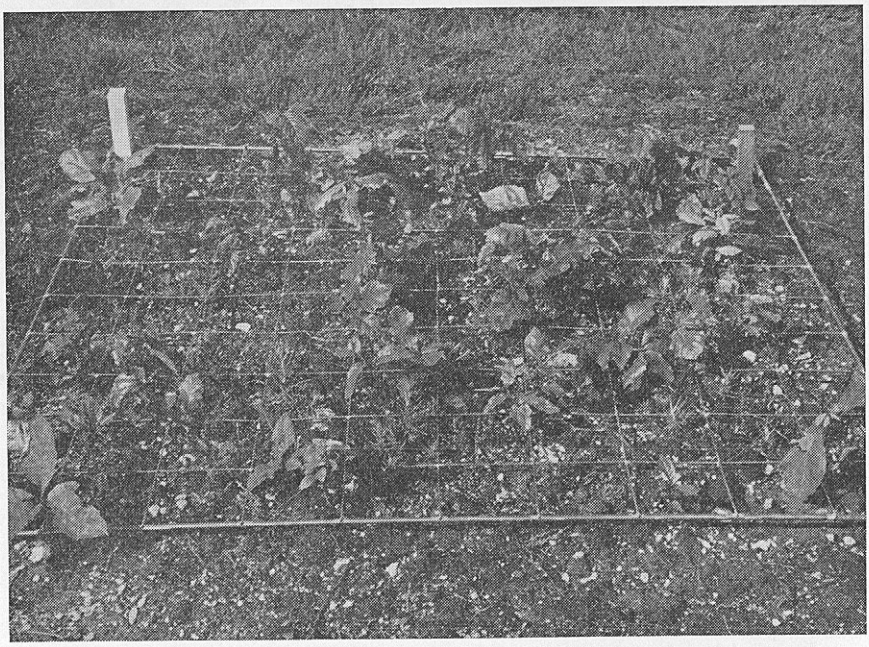
(*J. W. Kinnaird, E. Kemp*)

6. Grazing and the Regeneration of Shrubs and Trees

Management for wildlife conservation includes the creation and maintenance of diversity in habitat structure. One way of doing this in the uplands is to establish and perpetuate woodland and scrub communities. It is well known that the present scarcity and continuing depletion of natural tree cover in the Highlands is partly a result of uncontrolled grazing by red deer and domestic stock. Yet there is a complete lack of quantitative data on interactions between these animals and the regeneration of woody plants.

An initial approach to this problem was made on a representative area of red deer wintering ground at Glenfeshie in the central Highlands. The aims were (*a*) to define the pattern and severity of grazing on the vegetation, including saplings of birch and juniper *Juniperus communis*, between October and May, and (*b*) to find how this was related to snow cover and to the nutrient content and digestibility of the forage. Red deer were the most important herbivores in the glen; a few roe deer (*Capreolus capreolus*), rabbits *Oryctolagus cuniculus*, hares, sheep, cattle, and horses were also present but their influence was discounted.

When free of deep snow, the alluvial grasslands in the glen were heavily utilised until the supply of green herbage reached a low ebb in March; from then until the flush of new growth in May–June, grazing was light and sporadic



A four-month-old stand of mixed deciduous and coniferous seedlings grown from seed in a fertilised peaty-podsol at Glensaugh (quadrat 1m^2).

(Fig. 3). Heather was the most abundant plant on the range and was grazed throughout winter, but especially in November and April; although poor in nutrients, it is less susceptible to die-back than the grasses and is more available during snow. The scattered patches of juniper scrub provided excellent shelter and cover for deer, and the juniper shoots contained relatively high concentrations of nutrients. Nevertheless, browsing was more or less confined to December–February when snow cover was frequent and persistent.

Approximately similar proportions (79–90 per cent.) of juniper and birch saplings were damaged by browsing between October and June, but the patterns differed. Juniper saplings, like the mature bushes, were browsed

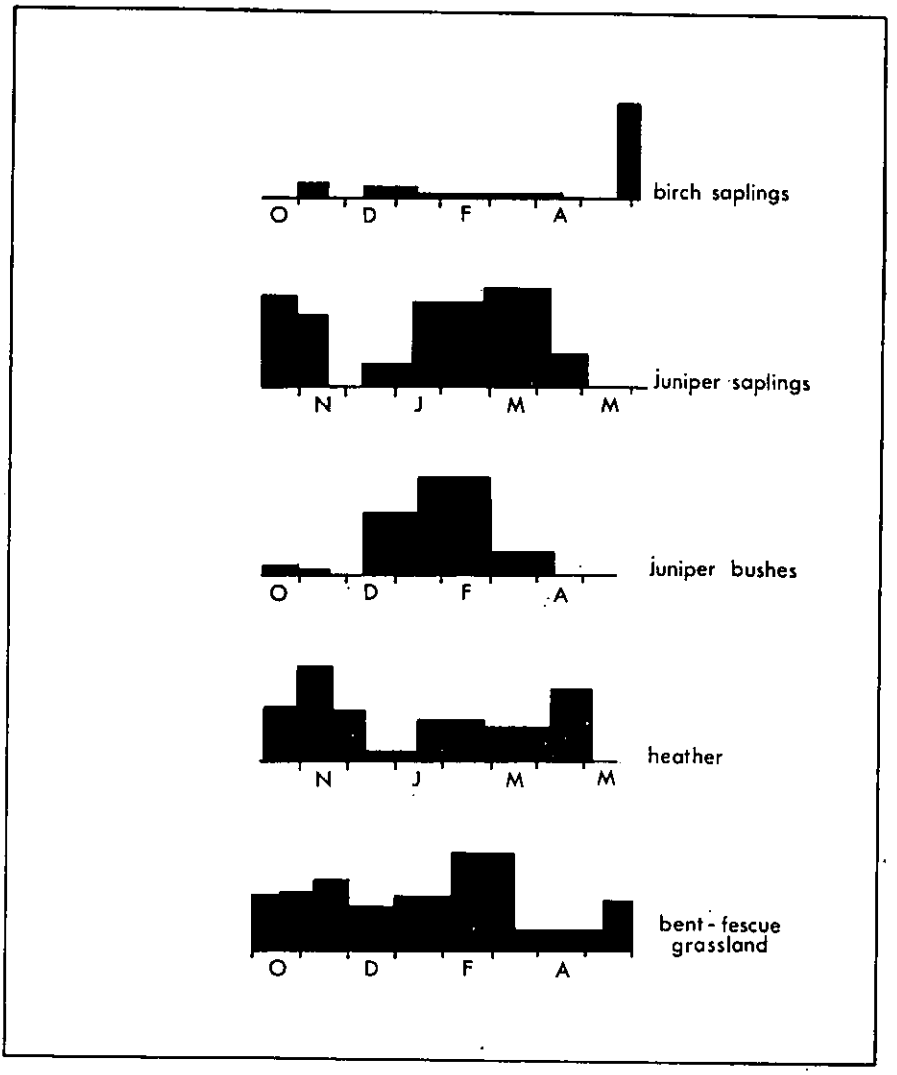


FIG. 3—Pattern of grazing on different types of forage at Glenfeshie, October 1968 to May 1969.

mainly during periods of snow cover and avoided at other times (Fig. 3). By contrast, birch was nibbled steadily from October to late May, when there was a sudden intensification of browsing as the buds burst. It seems that birch was grazed at random for most of the winter, and there is a linear relation between the rate of deposition of deer dung and the rate of browsing on saplings (Fig. 4).

Damage to young juniper and birch in October–May is probably a result of the high overall grazing pressure on the winter range rather than of positive selection by the animals. A partial reduction in deer numbers, or modification of their distribution, might be sufficient to allow woodland and scrub to develop. These possibilities will be investigated.

(G. R. Miller, I. A. Nicholson, D. McCowan, I. S. Paterson, T. Parish, C. O. Badenoch, R. P. Cummins, A. M. Miles, S. M. Moyes)

7. Study of Cattle Grazing in Relation to Vegetation Change

This work was started in autumn 1970 in Glenfeshie where cattle have been introduced in summer to improve the grazings on the red deer wintering range. Preliminary work, including a survey to determine the distribution of the cattle dung and the boundaries of the area utilised by the animals, has been completed.

Research on this problem will be extended to Rhum where cattle have recently been introduced. *(I. S. Paterson, R. P. Cummins)*

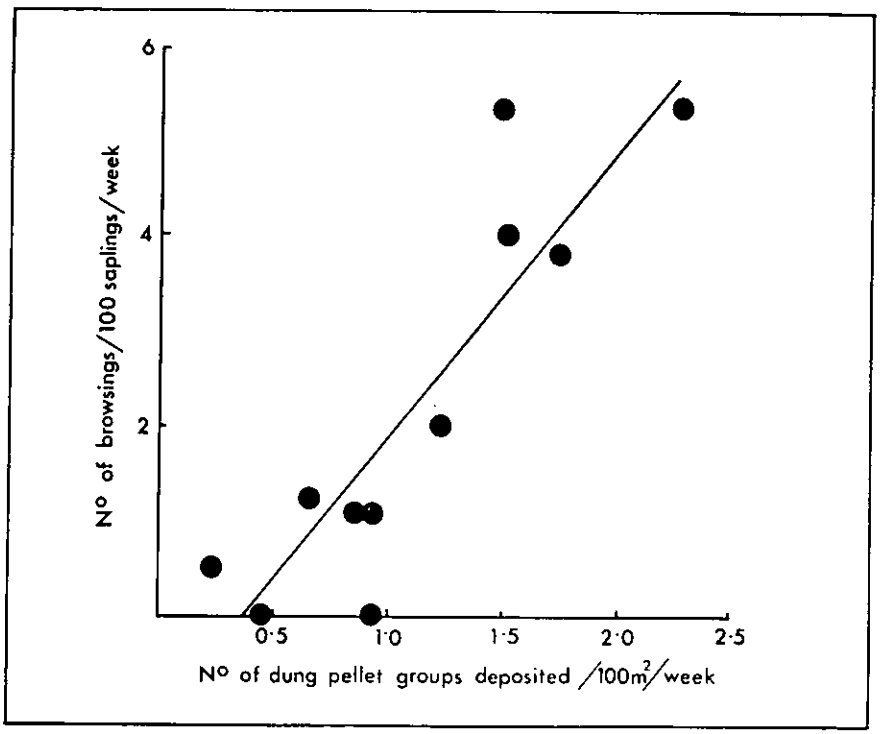


FIG. 4—Relation between rate of deposition of dung by red deer (D) and rate of browsing on birch saplings (B). B=2·97D—1·09

8. Burning Molinia-Dominant Vegetation for Grazing by Red Deer

Vegetation containing abundant purple moor-grass *Molinia caerulea* predominates in northwest 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 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, litter accumulates, masking the new growth in spring and creating a severe fire risk.

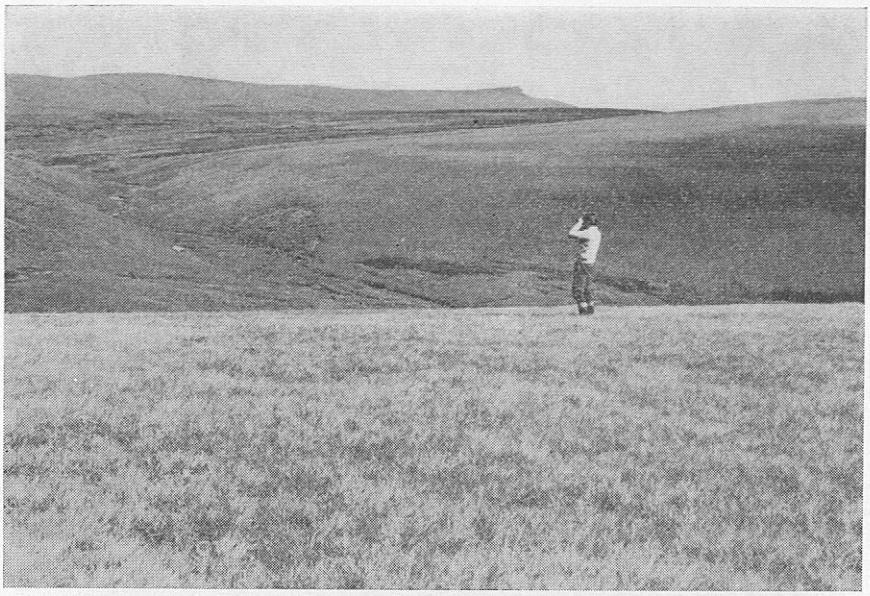
A study was made during 1967–69 of the grazing use by red deer of *Molinia*-dominated grassland and *Molinia*-rich blanket bog burnt experimentally in April 1967 on the Isle of Rhum National Nature Reserve. For ten weeks after the fire most of the deer seen in the area were present on the burnt ground. Estimates of deposition rates of faecal pellet groups and of the frequency of grazing of *Molinia* indicated that grazing was significantly greater on burnt than on unburnt ground through the spring and early summer after the fire, and decreased significantly during the summer, being relatively light by the end of July. The grazing frequencies suggest that a month after the fire grazing on burnt ground was from 6–18 times heavier than on adjacent unburnt ground. Grazing on burnt ground declined sharply a year after the fire to less than twice that on the unburnt ground, but was not significantly reduced again in 1969. Eighty to eighty-five per cent of the litter was burnt, but two years later litter on the burnt ground had increased to nearly half that present before the fire.

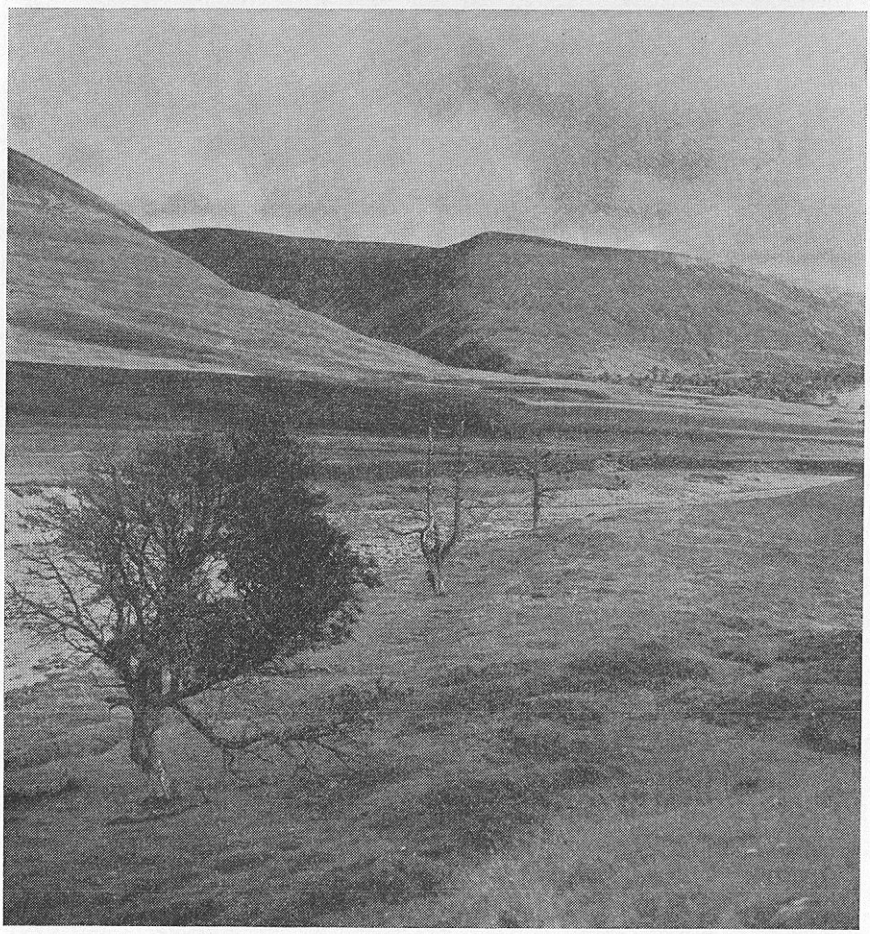
Thus burning made the new growth of *Molinia* considerably more attractive to deer. It is, however, an inefficient form of management. Its effects are shortlived and it also favours *Molinia* at the expense of *Calluna*, hence increasing the need to burn. Certain types of grasslands can be converted to *Agrostis-Festuca* grasslands through intensive grazing, but the grazing utilisation of *Molinia*-rich blanket bog presents a dilemma to which there is no ready solution. It is very extensive in the northwest, 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 red deer or other herbivores at the 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* at the expense of *Calluna*, reducing winter grazing and increasing the need to burn. Creating *Calluna*-dominant stands in places, and establishing scrub in others, would provide a greater diversity of forage and may be a partial answer to this problem, but as yet it is not known how this can be achieved.

(*J. Miles*)

9. Ecological Effects of Recreation on Cairngorm

Studies have been made of the impact of skiing developments on Cairngorm, as the first stage of a wider investigation into the problems of recreation in upland areas. A great increase in skiing activity has occurred on Cairngorm since 1960, when a road was made to 650 m and permanent uplift facilities were provided. Damage to vegetation and soils has resulted particularly from the construction of these installations, but also from the increased recreational





Glenfeshie showing summer—above (approx. 1,000 m)—and winter—below (approx. 300 m) —ranges of red deer.

use made of the hill. The studies described here were concerned with monitoring damage to vegetation, with defining causal relationships and with examining techniques for renovating damaged ground.

Maps showing the extent of damaged ground were made in 1968 and have been revised annually. The most serious damage was ground completely stripped of vegetation and frequently showing compaction or disturbance of soil profiles. The area affected (9 ha) included dirt roads and tracks, bulldozed pistes, and ground stripped by tracked vehicles. Several areas of bared ground, eroded by rain, formed the points of origin of sediment fans stretching many metres downslope. About 3 ha were affected by sediment deposition. Most plants liable to burial by sediment are short heath species, usually only a few cm high. Few can grow through even a thin covering, and *Carex bigelowii* was the only species found to make active growth through the gravel.

Most damage to vegetation, which took the form of bruised, broken and dead plants, and occasional patches of bare soil, was attributable to disturbance by skiers and occasional walkers. Ten to twelve ha of ground were damaged in this way. Observations on a small study area used intensively for skiing showed that damaged vegetation occurred on small patches of ground that became snow-free during thaws or as a result of wind or ski erosion. Uneven ground, particularly where there were prominent hummocks and ridges, was more severely damaged than relatively smooth slopes.

Walkers differ from skiers in generally being more restricted to the vicinity of paths. Moreover, the physical impact of walkers' footwear differs considerably from the slicing action of skis. The effects of trampling on vegetation were examined by describing gradients of damage and corresponding distributions of people in the field, and by simulated trampling experiments. An example of the latter approach is given in Fig. 5 which illustrates the responses to trampling of two component species of a wet *Calluna-Trichophorum* heath community. Damage to *Trichophorum* increased steadily with increasing trampling, but plants were not killed, and new growth in the subsequent two years masked the damage, so that total cover before and two years after trampling was more or less unchanged. Damage to *Sphagnum* hummocks showed evidence of saturation at a level of about one-third of the total trampling. It took the form of fractured shoots, and since growth in this species is almost entirely apical, recovery to a compact hummock was extremely slow.

Most people follow paths when these are available, as they are generally easier to walk on than vegetation. Paths were studied to ascertain (*a*) the relation between terrain and path width, and (*b*) the use made of paths by walkers. Several characteristics were correlated with path width. In particular, increases were associated with surface wetness, and with increasing surface roughness. Width also increased with angle of slope along paths but decreased with increasing roughness of adjacent ground. Observations of walker behaviour showed that the mean pace length of walkers declined as angle of slope increased, and pace length was shorter downhill than uphill. The impact of feet when coming downhill was also greater than when travelling uphill on the same slope. A study of one Cairngorm path revealed that 83 per cent. of persons walking uphill were on the path, but only 55 per cent. of those walking downhill. Several of these points suggest that damage is more likely with downhill than uphill walking. This may have application in the design of nature trails.

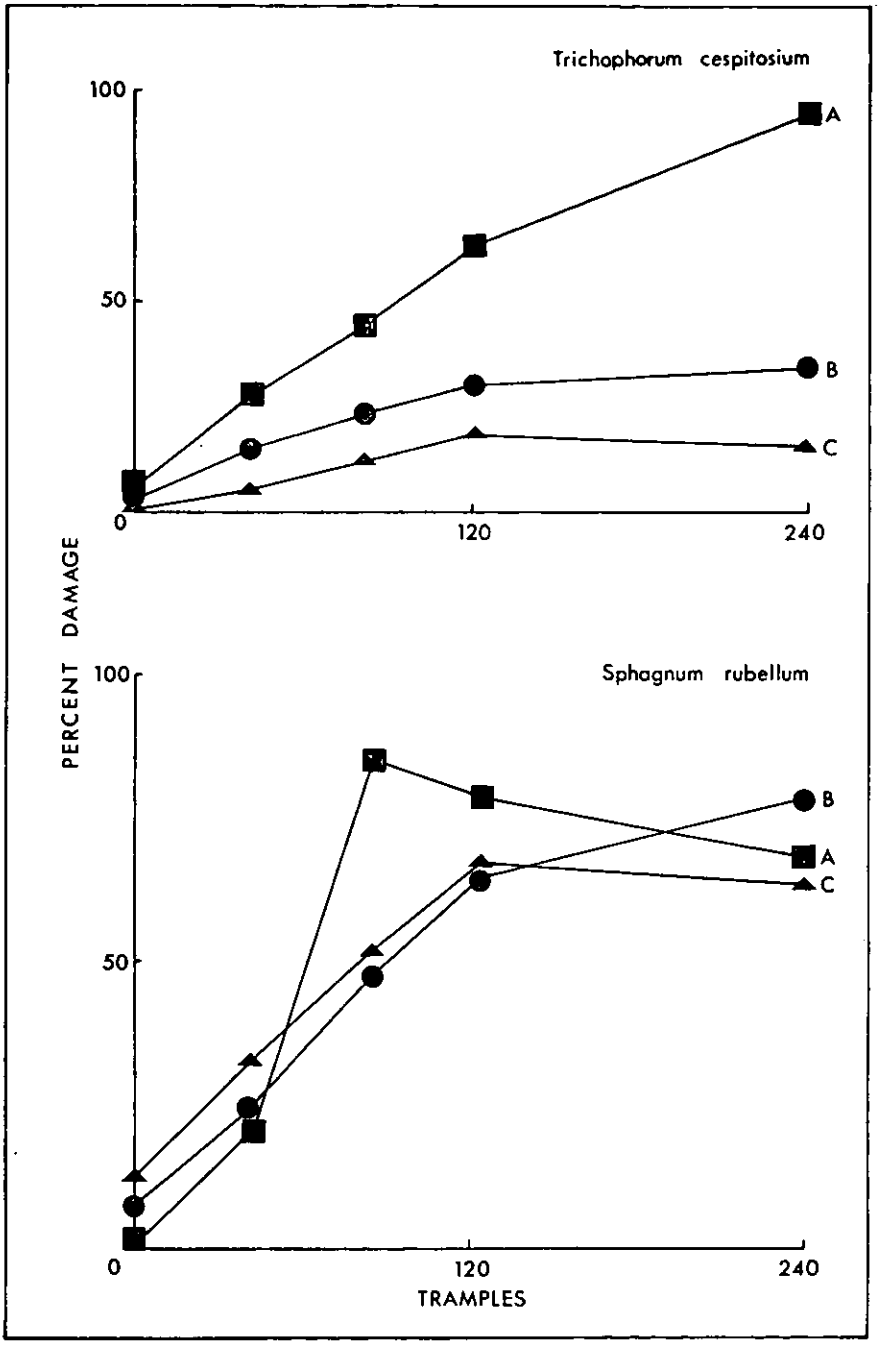


FIG 5—Effects of trampling on two species. Damage as percentage of cover of each species. Visual estimates A2, B12, C23, months after trampling.

Reseeding of badly damaged ground has been undertaken by the chairlift operators using a mixture including S.50 timothy *Phleum pratense*, Canadian timothy, creeping red fescue *Festuca rubra*, smooth stalked meadow grass *Poa pratensis* and New Zealand crested dogstail *Cynosurus cristatus*. The ground is first treated with ground limestone, basic slag and compound fertiliser. On sites suffering from erosion, bitumen emulsion may be sprayed to provide a 'skin' over loose soil. The worst damage along all except one of the uplift lines has been seeded in the last four years, but outlying patches remain. In general the cover resulting from seeding declines with altitude. In 1969, the plant cover on reseeds at 1,100 m was 48±23 per cent., and 83± 12 per cent. at 700 m, with proportional values at intermediate altitudes. Bryophytes established well on most reseeded ground (cover 24–39 per cent.) even on swards only one year old. The species present were generally those of the surrounding indigenous vegetation. Above 800 m, few seedlings of indigenous species were seen, but below this altitude larger numbers were recorded. The great majority were *Calluna*, and recolonisation was most pronounced on a reseed on peaty soil at 700 m. In addition to monitoring reseeded ground, various small plot experiments were laid out to test alternative seeds mixtures, soil stabilisers and other rehabilitative techniques.

The management problems on Cairngorm are largely those of controlling further damage by machines and improving the amenity value of the hill. Reseeding of damaged ground is quite feasible. Although the product—a grass sward—is not 'natural' it is probably satisfactory for a ski park, as it provides a vegetated surface, and prevents excessive erosion. The indigenous vegetation may return to the reseeded areas, but this is likely to be a lengthy process. Damage due to walkers can be reduced by canalising them along tracks or paths. Damage caused by skiers can probably be controlled only by confining skiing to areas completely snow covered, but this is unlikely to be practicable. (*N. G. Bayfield, I. S. Paterson, S. M. Moyes*)

10. Survey of Damage by Deer in Plantation Woodland

In collaboration with the North Scotland Conservancy of the Forestry Commission a survey of deer damage in plantation woodland was begun in 1970. The aim was to determine the nature and degree of damage to forest trees in relation to conditions of the environment. Fourteen forests, mainly in the west Highlands, were selected for study. It was also hoped to identify suitable areas for future experimental work. Although the survey has not yet been completed, several points of interest have emerged.

Red deer were present in all the forests and roe deer in all but one. All the forests except one were completely deer-fenced and though many fencelines were in poor repair, they generally acted at least as partial barriers to the movement of large animals.

An attempt was made to characterise habitat conditions both inside and outside plantation blocks. It was impracticable in the time available to make direct estimates of deer numbers, but simple indices of utilisation were employed and assessments made of the intensity, extent and distribution of damage.

The four main types of damage by deer were: browsing, bark-stripping, threshing and rubbing. Damage was widespread though the total amount was not great. A wide range of indigenous hardwoods was browsed, though birch

and willow *Salix* spp. probably provided the bulk of the hardwood browse. Alder *Alnus glutinosa* was less commonly attacked than the other species. All species of planted conifer were browsed, but Scots pine *Pinus silvestris* was generally the least affected. Most browsing had occurred outside the main growing season. Bark-stripping was less prevalent than browsing and was found mainly in pole stage stands. Damage occurred mainly within 15 m of the forest edges or in areas with open spaces. There was little evidence that any of the damage had occurred during the growing season. Lodgepole pine *P. contorta* and Norway spruce *Picea abies* were the most frequently attacked and the most severely damaged commercial species, though a wide range of species including hardwoods was affected. Both rubbing and threshing were comparatively minor forms of damage.

Further relationships between damage and various habitat characteristics may come to light when the data are fully analysed. But in none of the damage forms was there any evidence that either the intensity or extent of damage was simply related to the density of red deer.

(C. O. Badenoch, I. A. Nicholson, G. R. Miller)

11. Red Deer Dispersion Studies

Important problems associated with red deer management today are how deer distribute themselves within the habitats they occupy and how this dispersion is brought about. Deer compete for land, particularly in winter, with other interests such as conservation (e.g. by preventing regeneration of the Caledonian pine forests), forestry and agriculture and can cause considerable damage. Before we can have rational deer management (for whatever end) it is clearly important to understand the factors that affect deer dispersion. The main ones are the animals' needs for food and shelter, and intraspecific interactions between the deer themselves resulting, for example, in the separation of stags and hinds into geographically different areas. This is important for management because stags, which are a very important asset to the deer-forest owner, tend to occupy the lower end of a glen system in winter where they often conflict with other land interests. We decided, therefore, to study the reasons for, and the mechanisms underlying, the separation of stags and hinds in winter as one important aspect of deer dispersion.

The initial step was to document this separation more fully using a single 'case-history' approach. It was also hoped that an exploratory study would enable hypotheses to be framed concerning deer dispersion over a broader field. The study started at Glenfeshie in late January 1970 and this summary refers to the period up to the beginning of June 1970.

Separation of the sexes (Table 2) was not complete but was most clearly defined in May/June and least in March. In undisturbed groups there was a tendency to find fewer stags as the number of hinds in the group increased.

The sexes overlapped in their overall ranges but the areas of concentration were different. Moreover, on any one day there appeared to be a tendency to find either one sex or the other in the area of overlap, rather than both. There was a tendency for hinds to move out of the main glen system in spring but stags moved up it into the areas previously occupied by hinds.

The work is continuing with emphasis being placed on the setting-up and the breakdown of the winter ranges. We also intend to look more closely at the spacing of animals within, as well as between groups.

(B. W. Staines, T. Parish)

TABLE 2. Group sizes of deer in Glenfeshie and percentage of stags observed without hinds in January–June 1970

Month	*No. visits*	*Mean no. of deer counted per visit*	*Mean no. of groups seen per visit*	*Mean group size per visit*		*Percent. stags without hinds* *I*	*II*	*III-V*
January	2	637	26	25		10·9	51·1	66·7
					n	265	92	213
February		660	26	25		24·3	61·9	72·8
					n	481	194	217
March		1,040	30	35		15·0	44·1	50·7
					n	921	356	737
April		674	23	29		29·1	52·1	59·0
					n	525	420	680
May/June		474		23		39·6	77·0	86·9
						426	248	893

Notes—1. Classes of stags refer to different categories recognised in the field. These are based on body and antler size.

2. Class I refers to stags with knobs and short spikes. Class V comprises antlerless adults (i.e. hummels and stags that had cast their antlers).

12. Annual Cycles of Condition and Body Composition in Selected Classes of Red Deer on the Isle of Rhum

Red deer are ecologically and economically important in the Scottish Highland scene. However, the 2·8 million ha of land occupied by deer shows widespread effects due to heavy grazing. Similarly, the deer themselves—numbering about 180,000–200,000, annually yielding 30,000 carcases and supporting the sport of stalking—show relatively poor growth and breeding characteristics. There are thus two related management and conservation problems: 'carrying capacity' and deer performance. In research terms, we need to know more about the impact of red deer in Highland habitats and how such habitats meet the requirements of red deer. As one of the main starting points in the analysis of these problems, a project began on the Isle of Rhum in April 1969 to describe the body composition and condition of selected classes of red deer throughout the year. This work is scheduled to last two years and involves assessments by measurement, dissection and chemical analysis of about 280 deer. The four classes of red deer chosen for study were mature stags, mature 'yeld' hinds (those with no current year's calf), and milk hinds with their calves. Three of these classes represent fully grown deer with known reproductive characteristics, and the calves represent animals capable of growth.

The field sampling programme is now complete, but only some data have been examined so far. Tables 3 and 4 summarise results from the first year on dressed carcase weight and on fat reserves. The following comments are of interest.

Red deer on the Isle of Rhum.

TABLE 3. Mean dressed carcase weights (kg) of deer shot on Rhum

	Sample Periods						
	Late April/ Early May	*Early July*	*Late September*	*Late October*	*Late November*	*Late February*	*Late March*
Stags	45	53	65	55	50	43	46
Yeld Hinds	34	37	43	45	45	34	38
Milk Hinds	30	36	36	37	35	32	29
Calves	19	Not measured	17	19	16	16	17

TABLE 4. Fat reserves (in kg) of red deer shot on Rhum

		Sample Periods						
		Late April/ Early May	*Early July*	*Late September*	*Late October*	*Late November*	*Late February*	*Late March*
Stags	Body fat	0·066	0·339	1·366	0·154	0·138	0·087	0·097
	Rump fat	0	0·243	0·793	0·002	0·019	0	0
Yeld Hinds	Body fat	0·065	0·162	0·725	0·673	0·862	0·422	0·344
	Rump fat	0·005	0·059	0·338	0·310	0·362	0·142	0·089
Milk Hinds	Body fat	0·054	0·064	0·184	0·093	0·135	0·057	0·076
	Rump fat	0	0·009	0·066	0·006	0·030	0	0·002
Calves	Body fat	0·019	Not	0·027	0·023	0·036	0·020	0·035
	Rump fat	0·001	measured	0·001	0	0·001	0	0

Mature stags reach their maximum annual body weight by late September. Mating behaviour (=the 'rut') starts in late September and lasts about four weeks. During this time, the stags are very active, their food intake is considerably reduced, and they show a considerable loss of body weight and condition. The change in live weight amounts to 17 per cent. and the amount of dissectable body fat declines by about 90 per cent. Stags continue to decline in weight and condition until a minimum weight (78 per cent. of the September value) is reached in March. Dissectable body fat declines correspondingly to about 7 per cent. of the September value. Body weight and fat start to recover in late April and May.

Both classes of hinds reach maximum body weight and condition in October and November and show a steady decline to a minimum in March and April. Hinds, particularly those pregnant, show a delayed resumption of growth and condition compared with stags. Pregnant hinds become next year's milk hinds and non-pregnant hinds become next year's yeld hinds. During the autumn, yeld hinds show heavier carcase weights, bigger fat reserves and much higher ovulation and pregnancy rates than milk hinds (see Table 5). Ovulation in hinds appears to be very much dependent on body weight and condition. Hinds in best condition ovulate first, whereas poorer hinds either ovulate later in the breeding season or fail completely. In typical Highland habitats around 40 per cent. of mature hinds fail to breed each year.

TABLE 5. Some characteristics of yeld and milk hinds

(a) *Weight data (kg)*

Period	*Item*	*Yeld*	*Milk*	$\frac{Milk}{Yeld} \times 100$ (*Per cent.*)
September	Dressed carcase wt	43	36	83
	Kidney fat	0·72	0·18	25
	Rump fat	0·34	0·07	19
October	Dressed carcase wt	45	37	82
	Kidney fat	0·67	0·09	14
	Rump fat	0·31	0·0	2
November	Dressed carcase wt	44	34	78
	Kidney fat	0·86	0·14	16
	Rump fat	0·36	0·03	8

(b) *Fertility* (November–April samples)

Pregnancy rates Yeld=85 per cent. pregnant.
Milk=48 per cent. pregnant.

(c) *Mean embryo weights (kg) in pregnant hinds*

	Yeld	*Milk*
November	0·0009	0·0006
February	1·157	0·847
March	2·150	1·980
April	4·659	3·648

This switch mechanism, actuated by condition, may be regarded as a useful survival characteristic—an animal in poor condition in autumn can better withstand the winter without the demands of pregnancy. This may have evolved in red deer as an alternative to embryo resorption or natural abortion in times of stress; embryo resorption and 'casting' seem very rare in Scottish red deer compared with many other mammals.

Red deer calves are born mainly in late May and June, though some births occur much later. Those born in the normal calving season show a rapid gain in live-weight up to October, with an increment of about six times their birth weight. However, from late October to March there is a complete growth check. Growth resumes in April. Throughout their first year of life red deer calves show very poor fat reserves; even in October the body fat is barely dissectable. So it is not surprising that calves show a high death rate. On Rhum, about 10 per cent of the calves alive in autumn die before their first birthday.

Later analyses of data from this project will concentrate on relating selected major life cycle features to chemical aspects of body composition. In addition, technical work on the correlations between different condition assessment procedures will provide a useful basis for later ecological projects which involve the condition of red deer.

(B. Mitchell, D. McCowan, G. Sturton, J. A. Stevenson, A. B. McLennan, W. Jenkins)

13. Nutritional and Physiological Studies on Captive Red Deer

Nutrition is probably the main limiting factor in the productivity of red deer in Scotland. We are aiming to study the performance of captive deer on high and low planes of nutrition to aid in assessing the nutritional status of wild deer. At first, we are working on the performance of lactating hinds and young calves. The experiments began in July 1970, and are being carried out at the Rowett Research Institute in collaboration with R. N. B. Kay.

Milk yield and composition. Two pregnant hinds were brought from Rhum in May 1970 and kept on a high plane diet. They calved in July and August (gestation periods 233 and 237 days); both calves were males. Milk yields were measured and samples were obtained for analysis. Feed intakes were recorded and were very high during lactation.

One calf died at a month old, and its dam was ill for a time. The normal hind yielded milk at an average of 1,850 g/day for the first 50 days, containing 6–8 per cent. fat and over 7 per cent. protein. The yield fell to about 700 g/day at 100 days and 500 g/day at 140 days, and then gradually tailed off. The fat content rose to 15 per cent. at the end of lactation.

This experiment will be repeated in 1971–72, to compare lactation records of well-fed and also of under-fed hinds.

Growth rates of red deer calves. The suckled calf from the above experiment grew at the rate of 355 g/day at first, attaining a weight of 75 kg at seven months of age. At this stage he was starting to develop antlers.

12 wild calves were brought in at a few days old and reared on cow's milk. They were weaned at 7½ weeks on to a high concentrate ration (barley-based) and split into two groups. Group I were given concentrate to appetite, plus 10 per cent. roughage. Group II were given 70 per cent. of the amount eaten by Group I animals at the same weight. 48 kg was taken as the finishing

weight. Two animals of each group were then slaughtered for carcase and feed efficiency analysis, and two will be used for a digestibility trial. The results are still incomplete.

After weaning, the Group I animals initially grew at a rate of 265–300 g/day. The males attained a weight of about 63 kg and the females about 50 kg at seven months of age: in the males, considerable antler development had begun. The Group II animals at the same age had reached only 40–50 and 38–40 kg respectively.

Even the underfed Group II animals compared very favourably with wild deer calves, and this experiment shows how extremely undernourished many wild deer are. (*P. Arman*)

14. Management and Development of a Deer Forest

Outline of the Project

Glenfeshie estate, extending to 17,400 ha and rising to over 1,067 m, lies in the western Cairngorms. In 1967, the owners, The West Highland Woodlands, granted the Nature Conservancy facilities on the estate for research on red deer and their range. The Conservancy also agreed to co-operate with the owners in the management and development of the deer forest.

The eastern half of Glenfeshie contains a substantial part of the Cairngorm National Nature Reserve. Thus, in addition to extending our research facilities, it became possible to link the management of the Speyside portion of the reserve with the management of the whole Glenfeshie forest.

Investigational work at Glenfeshie comes into three categories:

(*a*) Ecological research on red deer and habitat problems as part of the Conservancy's research programme in Highland Britain.

(*b*) Studies aimed at guiding the management and development of the estate itself.

(*c*) A case history investigation assessing effects of management changes on the ecology of a large upland area.

This summary deals only with (*b*) and (*c*).

Under former ownership Glenfeshie was operated on traditional lines as a sporting deer forest. Culling of the deer stock, especially the hinds, was light. This gave little control over the numbers and 'quality' of the deer, and no doubt contributed to the depletion of scrub and woodland cover. Hill sheep had access to the estate through grazing rights of long standing.

The principal development aims are (*a*) to reduce the deer stock and control their numbers and movements, (*b*) to increase the area of woodland, and (*c*) to integrate afforestation with deer management. Natural tree and shrub regeneration will be encouraged and the growth and composition of the alluvial pastures in the lower glen improved. Thus, although red deer are still regarded as the main asset, they will be managed with more regard to the ecological characteristics and conservation interest of the area.

It was necessary first to describe the more important resources of the estate. The vegetation has been surveyed and the soils mapped.* These and other surveys helped in the formulation of development plans and provided a base-line from which future changes can be measured. In 1968 it was agreed

* The soil survey was carried out by the Macaulay Institute for Soil Research whose co-operation is gratefully acknowledged.

to increase the hind cull to bring about a 25 per cent. reduction in numbers over 4–5 years, and particular categories of animals were specified for shooting.

Although 38 per cent. of land comprising 6,475 ha lies below 610 m, the area of natural woodland, including open pine and juniper scrub, is only about 445 ha. This all occurs in the main glen which runs through the middle of the estate. Most of the woodland and scrub is in poor condition and without regeneration it will decline rapidly over the next 50 years. The area of new woodland proposed is over 1,012 ha, with just over half in the main glen and the remainder in an outlying part of the estate where there is little shelter. Plantations containing a predominance of Scots pine will be opened to deer once the danger of browsing damage has passed.

About 100 ha on and around the alluvial flats have been treated with lime and phosphate and most of this has been sown with white clover. Because deer move to the high ground in the summer, growth of the lower pastures must be controlled by summer grazing. The free-range sheep stock has been removed, but cattle are now used in summer to condition the herbage for use by the deer when they colonise the low ground after the rut.

Apart from general surveys and monitoring, most of the botanical work in Glenfeshie has been dealt with in other accounts. Two studies on the red deer, although done specially to help in planning the development programme, are of general interest and are therefore outlined here.

Deer numbers and distribution in relation to afforestation

The numbers and seasonal distribution of deer in the main glen were studied to assist in the selection of areas for afforestation. Other objectives were to provide information for studies on tree regeneration, and to contribute to research on deer behaviour.

The area studied by day was that part of the main glen which could be observed by one person in one day, even in deep snow, and included all the plantable areas there. At night, the area observed was smaller, being limited by the range of a spotlamp from a Land-Rover on the track on the floor of the glen. Observations were made initially at intervals of three weeks, but were later increased to three per month. The dispersion of deer was recorded on a simplified 1/25,000 map.

The numbers of deer in the glen showed a marked seasonal cycle being high in November–May, and declining after late June. In winter, they fluctuated greatly according to the weather.

The most important consideration in selecting sites for afforestation was the availability of 'plantable' ground in the main glen. The policy was to use the zone between the pastures in the glen bottom and the upper limit of plantable ground. The siting of blocks was at first planned in relation to local knowledge of deer habits and the distribution of natural woodland. As observations on deer distribution became available, the location of the sites was reassessed.

Population dynamics and performance of red deer

This work has two main objectives:

(*a*) To monitor the characteristics of the deer for local management purposes.

(*b*) To investigate factors affecting red deer management throughout the Scottish Highlands by comparing deer at Glenfeshie with those elsewhere.

This account is concerned mainly with the first objective and the immediate concerns are (*a*) to get data on deer numbers and performance now so that future changes can be detected and evaluated, and (*b*) to monitor the effects of management, such as selective shooting, on the population.

Research activities comprise:

(i) Counts of the live population (as stags, hinds and calves of the current generation) done in spring and in summer.

(ii) Surveys of natural mortality—attempts to find and describe all natural deaths on the estate.

(iii) Collecting data (age, sex, carcase weight, condition and breeding status) from all shot deer.

Spring and summer counts are used to detect major seasonal changes in the deer population. Glenfeshie estate comprises one large deer catchment area with fencing acting as a barrier at the lower end. It is likely, therefore, that the winter population is more or less self-contained. However, the estate is only part of a much greater area of red deer summer range, with few natural barriers to movements.

Up to 1966, the overall cull was low compared with recruitment resulting in a high population, probably controlled by natural mortality and emigration. Shooting pressure has now been increased and the poorer hinds are being shot. It is too early for any consequences of these changes to be measurable.

Spring counts in 1967–70 average 674 stags, 1,059 hinds and 380 calves on the estate. The hind population appears resident but stags are supplemented by incomers in summer. Shooting pressure has been increased progressively over three years from 123 stags and 81 hinds to 138 stags and 263 hinds but there has been no substantial change in the deer population. Natural mortality was low over this period, with an annual average of 12 stags, 23 hinds and 31 calves. So the total annual mortality, even with heavier shooting, was never very different from the annual recruitment of 380 calves. In any case Glenfeshie is surrounded by other deer ground and it is therefore unlikely that the deer population on the estate would respond immediately to changes of shooting policy. Further counts will show a rate of decline attributable to shooting, or will give evidence of immigration. Either consequence will be of interest to deer management both at Glenfeshie and elsewhere.

Although a detailed analysis has not yet been made, it is clear that the growth rates of Glenfeshie deer are low, the average age at puberty is high and breeding success is low, compared with deer from elsewhere. Only 56 per cent. of the sexually mature hinds at Glenfeshie breed successfully each year, suggesting that a large proportion breed only in alternate years. Slow growth and slow recovery from the effects of breeding strongly suggest nutritional stresses. Current management is aimed at reducing these by reducing deer numbers and improving the range.

(*D McCowan, I. A. Nicholson, B. Mitchell, T. Parish, J. W. Kinnaird, D. Welch, J. Miles, I. S. Paterson, C. O. Badenoch, G. R. Miller, P. Macrae, G. Sturton, D. J. Maclennan, S. M. Moyes and A. Miles*)

Wetlands Research Group

N. C. Morgan

1. Introduction

The Wetlands Research Group is responsible for the Conservancy's research on freshwater and peatland habitats. 'Freshwater' covers the full range of open waters from large lakes and rivers to small pools and springs. The term 'peatland' is applied to all peat-forming systems (mires) including the valley-mires, raised-mires and fens of the lowlands, and extensive peat covered areas (blanket-mires) of the uplands.

Management and research on wetlands are integrated through a larger group, the Wetlands Habitat Team, consisting of members of the Research Group and representatives of the conservation staff familiar with the range of management problems arising in peatland and fresh water for England, Scotland and Wales. This group meets annually to consider the management problems of the regions, to discuss research priorities and the co-ordination of field and research work on Reserves and to seek the best way of providing advisory services. The meetings form a basis for future research planning.

Major conservation problems in fresh waters are the impact of recreation (such as power-boating, sailing, angling, waterside caravan sites), eutrophication (e.g. artificial enrichment from sewage, detergents, agricultural fertilisers), and the assessment of the effects of such recent proposals as pumping water for domestic and industrial use from chalk aquifers. The outstanding problem in peatlands is the management of fenland habitats to maintain early seral stages. Other problems include the effect of agricultural drainage on mire hydrology, the effect of fires on raised mires, the impact of visitors on the more fragile mire communities and the effects of eutrophication (due to fertilisers used in both agriculture and forestry). There is a continuous need for survey and monitoring as a basis for assessment of the conservation value of wetlands, defining management and detecting changes.

Since 1966 the Wetlands Research Group has made a significant contribution to the International Biological Programme at Loch Leven, Kinross. Here the aim is to measure production and production processes from the input of solar energy into the system along the food chains to trout, perch and tufted duck. This is a combined study involving the Freshwater Fisheries Laboratory, Pitlochry, the Wildfowl Trust, and staff from various departments in the Universities of Edinburgh, Stirling, St. Andrews, Dundee, Glasgow and Newcastle. The Conservancy is responsible for investigation of physical factors (including hydrology), algae, benthic invertebrates and tufted duck. Loch Leven is a National Nature Reserve, and the IBP study is giving us a far more detailed knowledge of the major plant and animal communities and their inter-relationships than is known for any other freshwater body on a Nature Reserve. It also defines the management problems. This will provide a firm basis for future research.

A survey of peatland sites throughout Britain has been carried out to assess the conservation value of a wide range of peatlands and select a National Nature Reserve series. A similar survey has been carried out for both standing waters and flowing waters and is nearing completion.

The section provides advice to conservation staff and answers queries on wetlands problems arising in the regions; it also advises outside bodies such as Planning Authorities. The queries range from the effects of discharge of mine water into a river to the design of conservation areas in newly created reservoirs.

2. Hydrology and Physical Limnology at Loch Leven

(a) *Standard physical observations*

Regular records of physical factors at Loch Leven are maintained and the results circulated to other workers. An official climatological station is situated very near to the loch and use is made of its records of air temperature and rainfall. Direct observations are made of total incoming radiation, loch surface temperature, extent of ice cover and stratification, wind and stream inflow. The work of measuring underwater light penetration is shared with M. E. Bindloss and A. E. Bailey-Watts.

Whenever possible, results obtained at Loch Leven have been correlated with the data from permanent observing stations in the area. Not only does this provide a check on the results obtained at Loch Leven but also it enables us to calculate long-term conditions at Loch Leven, prior to the IBP Project, and also any gaps due to instrument deficiency can be filled. This approach has proved successful.

(b) *Water balance*

Using a synthetic long-term inflow record generated from data for the River Devon, the average water balance of the loch has been calculated and the results are shown diagrammatically in Fig. 6. The outflow from the loch is completely controlled by sluices supplying mills downstream. This explains the irregular pattern of level fluctuations.

The ecological significance can be seen in Fig. 7. The average annual percentage water volume lost is 16 per cent. per month. This means that for the standing crop of algae to remain constant, the production must exceed the other losses (e.g. from respiration or grazing) by at least 16 per cent. on average and up to 22 per cent. in November. The relative concentration curve applies to the conditions of no external supply from rain or rivers and describes, for example, the declining concentration of an accidental pollutant. Fig. 7 shows that although the average annual input (streamflow plus rainfall on loch) is more than twice the loch volume giving a crude replacement time of just under six months, 26 months are required if the concentration is to fall to 1 per cent. of the original.

These mass balance calculations are being extended to include the case of varying inflow. Deductions based on a comparison of river and loch water chemistry can be complicated by lag and other effects due to the water balance, and more refined calculations are required.

(c) *Wave action*

The extensive shallow shore zone within the loch means that erosion due to wave action is likely to have an important influence on shallow water benthic production. This is being investigated by P. S. Maitland.

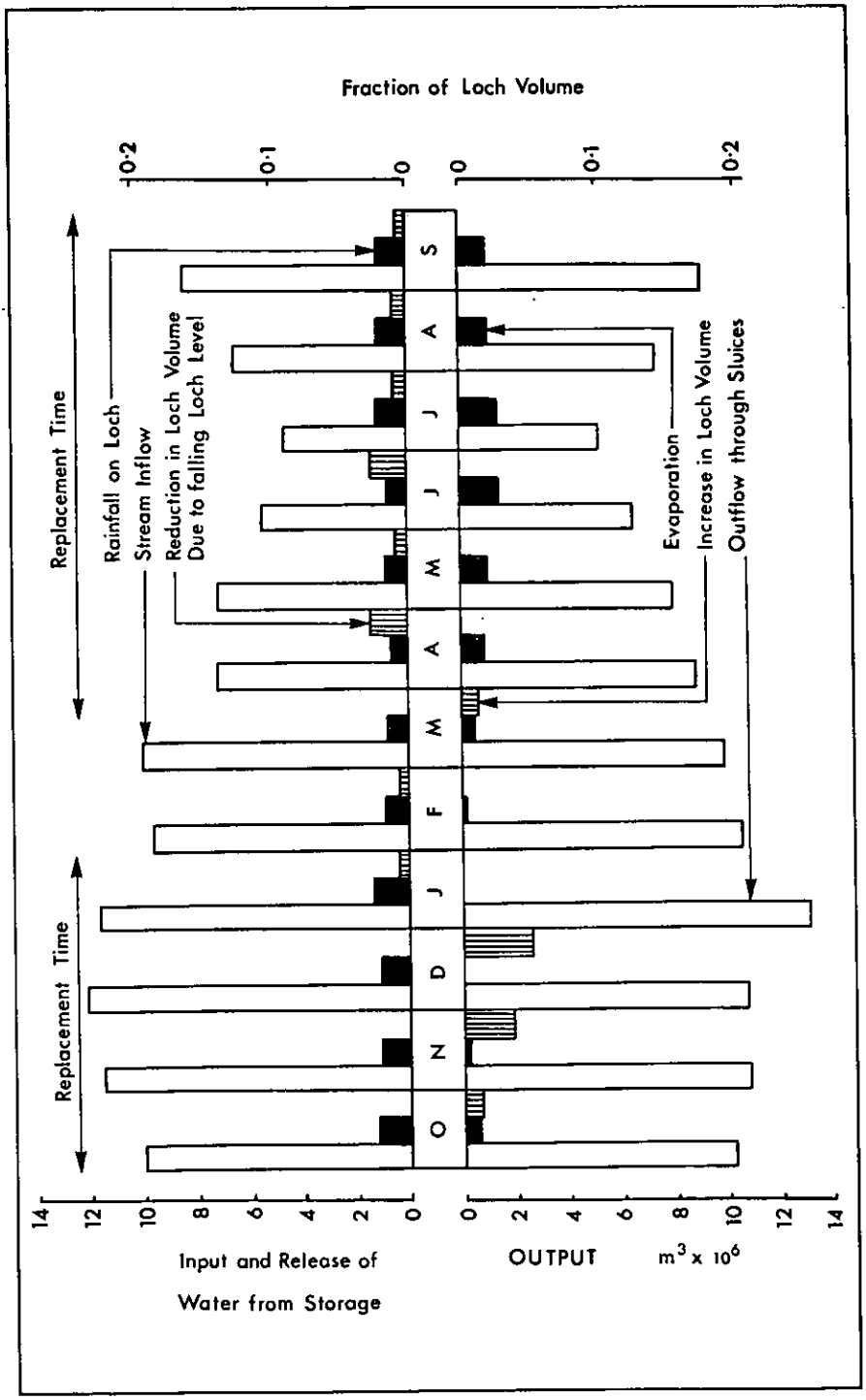


FIG. 6—Average annual water balance

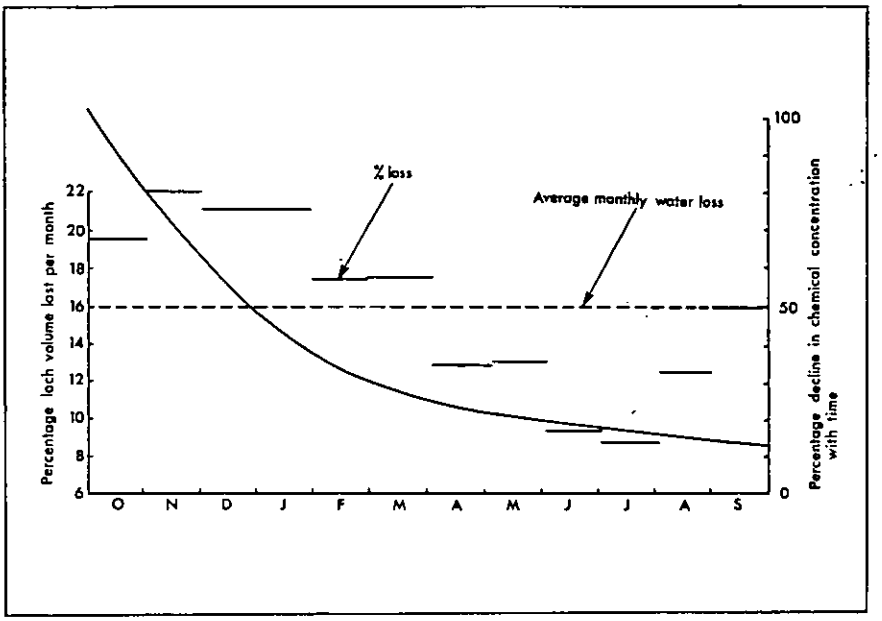


FIG. 7—Average monthly water loss by outflow from the loch (horizontal lines) and change in concentration which would take place for a dissolved substance which was not being replenished (curve).

In order to apply the results obtained at Loch Leven elsewhere we are concentrating on the actual physical processes rather than simply making observations of relative bed stability. The first essential is the ability to predict wave height and period knowing wind strength and fetch for open water conditions, i.e. where the bed has no influence. The way in which wave characteristics are modified by the influence of the bed is reasonably well established for marine conditions, and presumably such relations also hold in fresh water. There are also various equations which define the stress on the bed, given the wave characteristics. In this way it is intended to produce maps of relative bed stability in terms of wind strength. These can then be compared with standing crop changes.

Work has so far been concentrated on the measurement of open water waves using a simple anchored pole. This work is still continuing but it appears that the modified Bretschneider method, as described in the Beach Erosion Board Technical Memorandum No. 132, is reasonable at Loch Leven. The main problem in accurate wave forecasting seems to be the measurement of wind speed. Wind speed measured at the point of wave observation overestimates wave height while wind speeds measured at the upwind land station results in under-estimates.

(d) *Lake currents*

The wind-induced current system in any lake has an important influence on its ecology, particularly on its chemistry and phytoplankton. The whole concept of nutrient cycling requires a means of releasing nutrients from the bed and their dispersal throughout the water body. Diatoms and other algae

are fractionally denser than water and sink to the bed if not maintained in suspension by the current turbulence. Primary production estimates, being made in static enclosures, are subject to as yet unknown errors because of the absence of vertical motion of algae in and out of the light and possibly altered assimilation rates due to lack of turbulent mixing. This is being studied in the laboratory by M. E. Bindloss.

The character of lake currents is determined by the form of the general circulation, particularly by whether or not a bottom return current occurs. In long narrow valley lakes where water piles up at the down-wind end, the observed current results from the superposition of a wind drift current and an opposing gradient current so that a bottom return current occurs and speeds are low. In broad shallow lakes, where water is returned to the upwind end by a surface current, the lake current is a pure wind drift current and is faster than in the former case (Fig. 8). Observations of the surface circulation pattern and of the velocity depth profile have been made using drogues; but although the surface current pattern is not yet fully defined at Loch Leven, it is already clear that the currents on the loch are pure wind drift currents and that the circulation is one of complex horizontal rotations.

The form of the velocity/depth profile is almost like that of a river and this, combined with horizontal surface rotations, results in very efficient mixing. The mixing efficiency is demonstrated by the virtual absence of chemical and other gradients within the loch and the very temporary nature of any stratification.

Further insight into the ecological significance of the current system at Loch Leven partly depends on just how closely the velocity/depth profile resembles that of a river, in particular on the validity in Loch Leven of formulae for diffusion, sediment suspension and bed stability which have been derived for the logarithmic velocity profiles found in rivers and the lower atmosphere. Present work is concentrated on the analysis of the properties of lake current velocity profiles. *(I. R. Smith)*

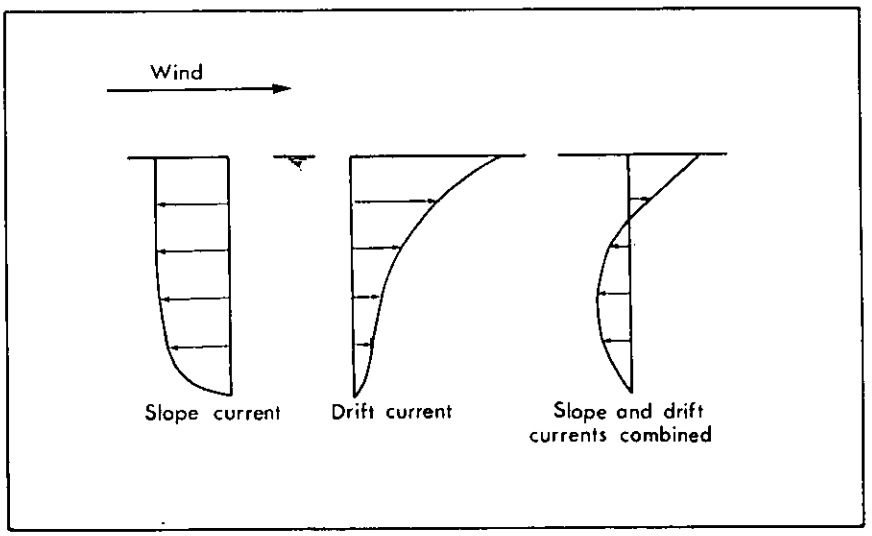


FIG. 8—The form of lake currents

3. Crops of Phytoplankton in Loch Leven

Studies on the ecology of the algae of Loch Leven have been mainly descriptive and observational although in 1970 I began experiments designed to interpret some observations. The main routine has been to identify the species of planktonic and benthic algae and measure the crops they produce. The resulting information is considered in relation to physical, chemical and other biological variables.

The algal crops are composed of populations of many species each behaving differently with respect to rate of increase or decrease, utilisation of nutrients and availability as food for various consumer organisms. The population densities of at least the predominant algae are estimated by counting their cells. This is done with inverted and conventional microscopes following concentration of the algae from measured volumes of water by sedimentation with iodine and potassium iodide solution which also stains and preserves the algae.

Another aspect of the work involves collection by centrifugation of large amounts (e.g. 500 mg dry weight) of phytoplankton material for chemical analysis of the plant cells themselves. Information on the carbon, nitrogen, phosphorus (and, in the case of diatoms, silica) content of the algal crops is obtained. This is compared with the levels of these chemical nutrients dissolved in the water, and indications of nutrient limitation are obtained together with a fuller understanding of the extent and rates of nutrient uptake. At

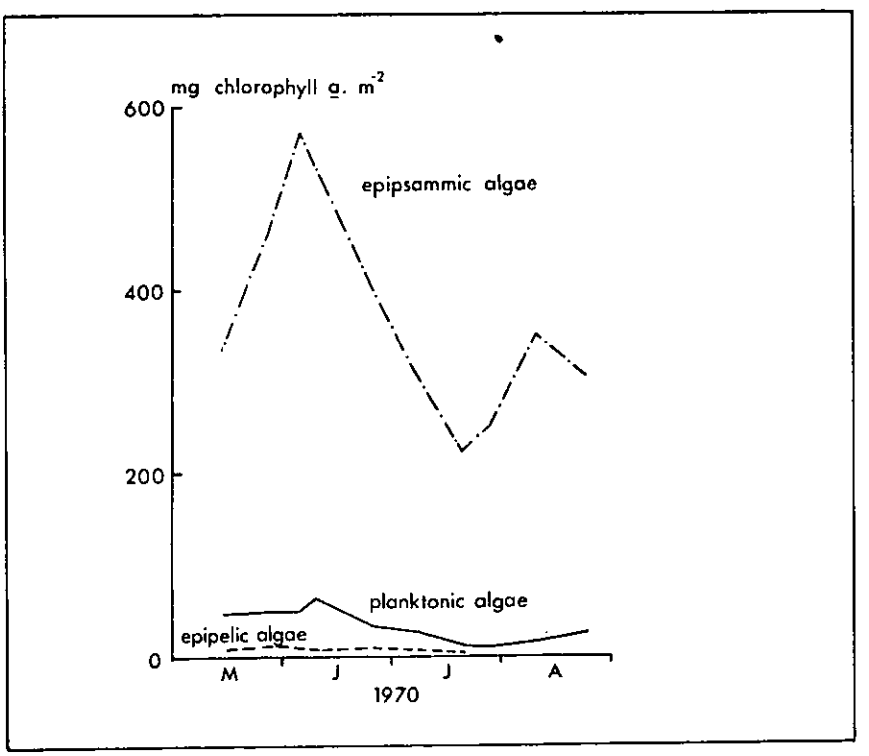


Fig. 9—Variation of epipsammic and epipelic algae in the top centimetre of sediment, and of planktonic algae in the overlying water column, as indicated by chlorophyll a concentration, at a shallow (0·7 m) station, May to August 1970.

certain times during this aspect of the work, difficulties have been experienced due to interference by other C, N, P and SiO_2-containing matter, e.g. protozoa, small rotifers, non-living and dead materials also suspended in the water of this shallow lake.

The results show that large crops of planktonic algae (equivalent to 10–260 mg chlorophyll a m^{-3}) are maintained through the year in Loch Leven and these are considered to be the main contribution to the lake's primary production. Although macrophyte growth is sparse, considerable quantities of benthic algae, mainly diatoms but including some blue-green and flagellate algae, develop as attached (epipsammic) and motile (epipelic) communities associated with about 50 per cent. of the sediment surface of this shallow water body. Studies have been carried out on the species composition, seasonal succession and spatial distribution of these benthic algae. Chironomid gut analyses have shown that they form an important food source for chironomid larvae, and they may also be an important factor to consider when interpreting changes in water chemistry, which are at present being analysed in relation to the planktonic community. Despite the common occurrence of wind-induced mixing which disturbs sediment material, the amounts of benthic algae introduced into the water column rarely contribute significantly to the open water chlorophyll a values.

More than 200 species of planktonic algae have been recorded. Several dozen species are always present but usually one or a few predominate. The most important species in terms of live cell volume and fresh weight are shown in Table 6, which gives the sizes and times of their population maxima and their mean single cell volumes. This shows that the species succession since January 1968 is complex, with the dominant species occurring over similar periods of successive years often belonging to different taxonomic classes. This complex succession, possibly reflecting an unstable environment, is difficult to relate to observed changes in environmental variables, since different algal species may react in different ways.

The predominance of small 'nanno' algae ($<10\ \mu m$) and small cells of other species is an interesting general feature. This may be associated with the apparent rarity of filter-feeding herbivorous crustaceans in the zooplankton, although algal-feeding protozoa are often abundant.

Fig. 10 shows the seasonal succession of chlorophyll a content of Loch Leven water. Values plotted are fairly representative of the whole open water mass and outflow of the lake. High population densities are maintained over most of the year, and even at mid winter crops are considerable. For comparison, Talling (1960, *Wetter u. Leben*, **12**) has revealed chlorophyll a maxima of less than 8 mg m^{-3} in Windermere during the spring of 1959, and he (Talling 1965, *Mem. Ist. Ital. Idrobiol.*, **18**) plots values of less than 11 mg m^{-3} in the North Basin of Windermere in August 1964. However, Ridley (1970, *Soc. Water Treatm. and Exam.*, **19**) quotes values of 20–100 μg chlorophyll a per litre ($\equiv$mg m^{-3}) for reservoirs storing R. Thames water.

Although the chlorophyll content of different algae varies, work on a variety of crops in Loch Leven shows that 4 mg chlorophyll a m^{-3} are equivalent to approximately 1 mm^3 live algal cell volume per litre. Where one species has strongly dominated the plankton for a number of weeks, e.g. *Synechococcus* n. sp. in mid summer 1968, and *Stephanodiscus astraea* in the autumn of 1970, the chlorophyll a to cell volume ratio has apparently varied with changing nutrient conditions and growth rates.

TABLE 6. Mean cell volumes (mcv in μm3) and maximum population densities (mpd in thousands of cells per ml, except for *Oscillatoria redekei* which is expressed as thousands of trichomes per ml) of dominant phytoplankton species 1968–70

	1968		*1969*		*1970*	
	mcv	*mpd*	*mcv*	*mpd*	*mcv*	*mpd*
January–April	Diatoma elongatum		C. pseudostelligera		C. pseudostelligera	
	470	13·7	200	126	200	56
	Asterionella formosa		Oscillatoria redekei		Steiniella sp.	
	450	6·8	50–200	59	20	26
	Synedra ulna		Diatoma elongatum			
	1,000	3·0	470	12·3		
May–July	Synechococcus n. sp.		Oscillatoria redekei		Steiniella sp.	
	10	5,000	50–200	750	20	200
			Diatoma elongatum		Synechococcus n. sp.	
			470	41	10	1,050
September–November	Cyclotella pseudostelligera		Dictyosphaerium pulchellum		Stephanodiscus astraea	
	200	14	65	232	1,000	27
	Oscillatoria redekei					
	50–200	15				

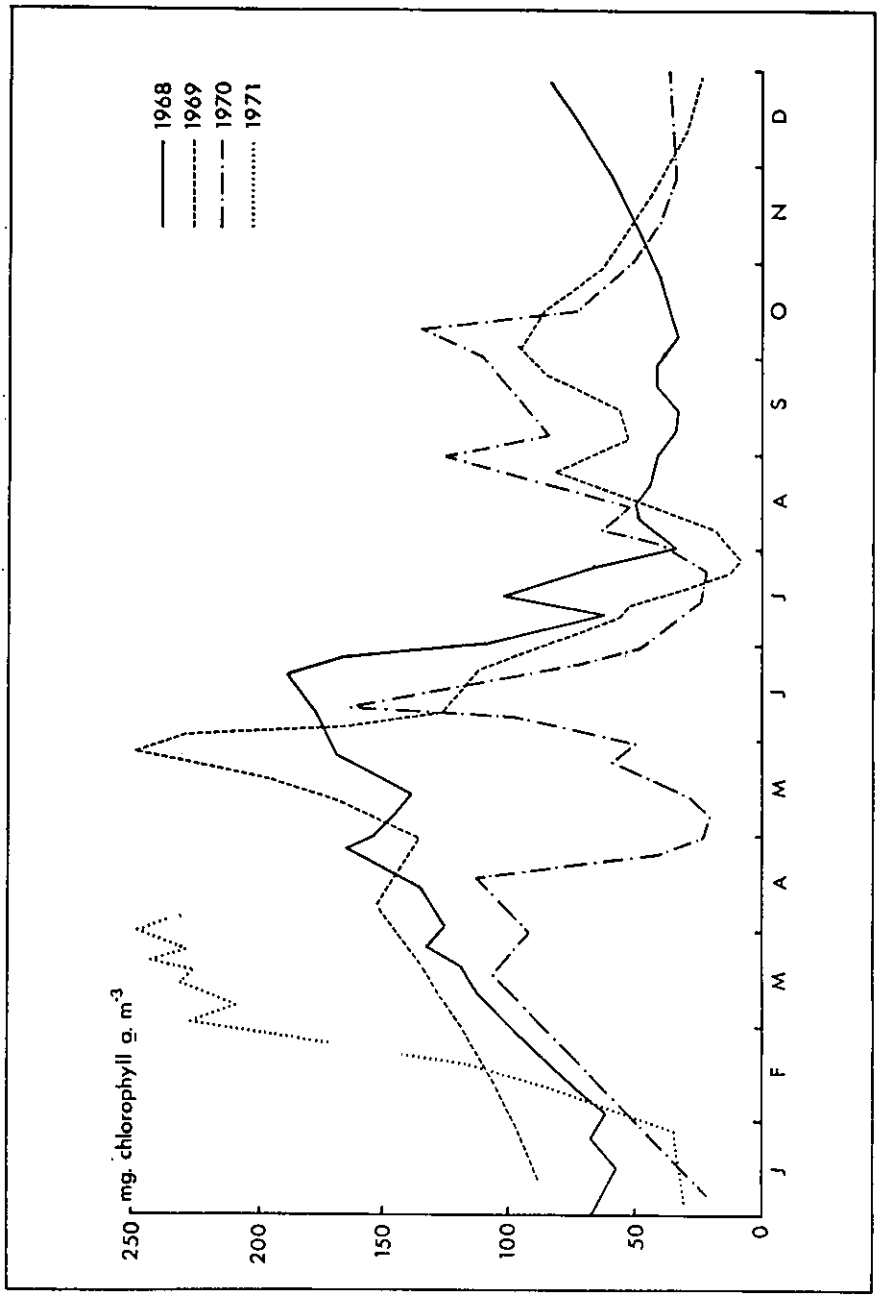


FIG. 10—Variation of total phytoplankton, as indicated by chlorophyll a concentration, in the 0-4 m column in open water, 1968-71.

Chlorophyll a also represents approximately 1·5 per cent. of the total dry weight, higher values being obtained with green algae and lower values with somewhat heavier diatom algae which possess a high silica content.

Having gained information on the seasonal changes in the quality and quantity of the algal crops it is necessary to investigate the factors possibly effecting these changes. Most experiments so far have concentrated on detecting nitrate-N, phosphate-P or silica limitation. Consideration of day length and temperature has been made in conjunction with these experiments and observations have been made on protozoan grazers and fungal parasites. Other studies concern the algae associated with the bottom sediment surfaces; at some shallow stations these algae often form very large populations (Fig. 9) which are probably competing with the plankton algae for the same inorganic nutrient sources.

Future work is planned to include more experimental investigations of algal/chemical relationships and the role of animals grazing the phytoplankton. It is hoped that polythene enclosures of up to 2,000 litres capacity can be established in the lake for these purposes. More detailed growth and nutrition studies will be made on one or two of the algae that have produced the largest crops in Loch Leven in recent years, e.g. *Synechococcus* n. sp., and *Cyclotella pseudostelligera*, if cultures of these can be obtained.

(*A. E. Bailey-Watts*)

4. Phytoplankton Productivity at Loch Leven

This work began in November 1967 and has two main aims:

(*a*) To calculate production rates of phytoplankton on hourly, daily and yearly bases. These values will be considered in relation to incoming light energy and in relation to energy demands of the consumers in an attempt to define food chain efficiency.

(*b*) To determine the factors controlling rates of primary production.

Photosynthetic productivity of phytoplankton is measured at weekly intervals from the changes in dissolved oxygen concentration between clear and darkened bottles suspended at various depths. From the distribution of photosynthetic rate per unit volume with depth, the rate of photosynthesis below unit surface area is calculated by integration.

Daily and yearly rates are calculated from the hourly rates (measured during short (*c.* 3 hour) exposure periods near midday) using general equations (Talling 1957, *New Phytol.*, **56**, 133–149).

Hourly rates of photosynthesis per unit area range from 69–1,586 mg O_2 m^{-2} h^{-1}. Values of less than 100 mg O_2 m^{-2} h^{-1} have been found only in December–March. Between March and October, values generally lie above 500 mg O_2 m^{-2} h^{-1}. For 1968, average daily gross photosynthesis is 5 g O_2 m^{-2} day^{-1} ranging from a maximum of 11 g O_2 m^{-2} day^{-1} in June to a minimum of 1 g O_2 m^{-2} day^{-1} in December. On this basis, annual gross production is 2 kg O_2 m^{-2} $year^{-1}$ which is equivalent to 7,194 kcal m^{-2} $year^{-1}$. Energy available for photosynthesis in the spectral region 400–700 nm is assumed to be 46 per cent. of total incident solar energy (Talling 1957, *New Phytol.*, **56**, 1–132). Thus 1·1 per cent. of the total incident radiation energy (or 2·4 per cent. of the energy available for photosynthesis) is utilised annually by the phytoplankton.

Seasonal changes in photosynthetic productivity are interpreted in relation to light intensity, light penetration, the light/dark regime imposed by water movements (in conjunction with I. R. Smith), temperature, crop density, *p*H and CO_2 supply and nitrogen and phosphorus availability.

Gross photosynthesis below unit area is at times poorly coupled to phytoplankton density due to (*a*) self-shading (*b*) an inverse relationship between phytoplankton density and its photosynthetic capacity (P_{max}, the light-saturated rate of photosynthesis per unit crop expressed as chlorophyll a). Net productivity may be further uncoupled by rising respiratory losses in dense crops.

Self-shading

Increase in crop density causes a reduction in light penetration and therefore a reduction in the depth to which photosynthesis can occur (the euphotic depth). Thus at high population density (217 mg chlorophyll a m^{-3}), the euphotic depth is reduced to 1·2 m from a maximum of 7·4 m at low population density (27 mg chlorophylla m^{-3}).

The phytoplankton itself imposes a limitation on further increase in productivity per unit area which might be expected from an increase in crop density.

The relationship between phytoplankton density and photosynthetic capacity (P_{max})

Throughout the year, P_{max} variations appear broadly correlated with those of temperature. At times, however, particularly during periods of rapid population increase, the overall trend of increasing P_{max} values with temperature is obscured. This is illustrated (Fig. 11) by the maintenance of relatively low P_{max} values between April and early June 1969, when the population was increasing, despite an increase in temperature from 6–18°C. During periods of high and increasing population density it appears that factors other than temperature regulate photosynthetic capacity.

As the population declined photosynthetic capacity increased markedly even though no further increase in temperature occurred.

This inverse relationship between population density and photosynthetic capacity tends to oppose the expected decrease in productivity per unit area with decreasing standing crop and thus tends to reinforce the self-shading effect in reducing variation in production per unit area.

Between November 1970 and March 1971 a further good example of an inverse relationship between crop density and photosynthetic capacity was recorded (Fig. 12). In this case (and in contrast to the situation in 1969), increase in population density was accompanied by a decline in P_{max} but again over a period of relatively constant temperature.

Other factors besides temperature may explain variations in photosynthetic capacity, and particular attention has been given recently to investigations on the influence of *p*H and of nitrogen and phosphorus supply on photosynthetic capacity. During both the periods discussed above lower P_{max} values were associated with high *p*H values. Laboratory experiments on the effect of lowering *p*H (by blowing in lung air) on P_{max} were carried out.

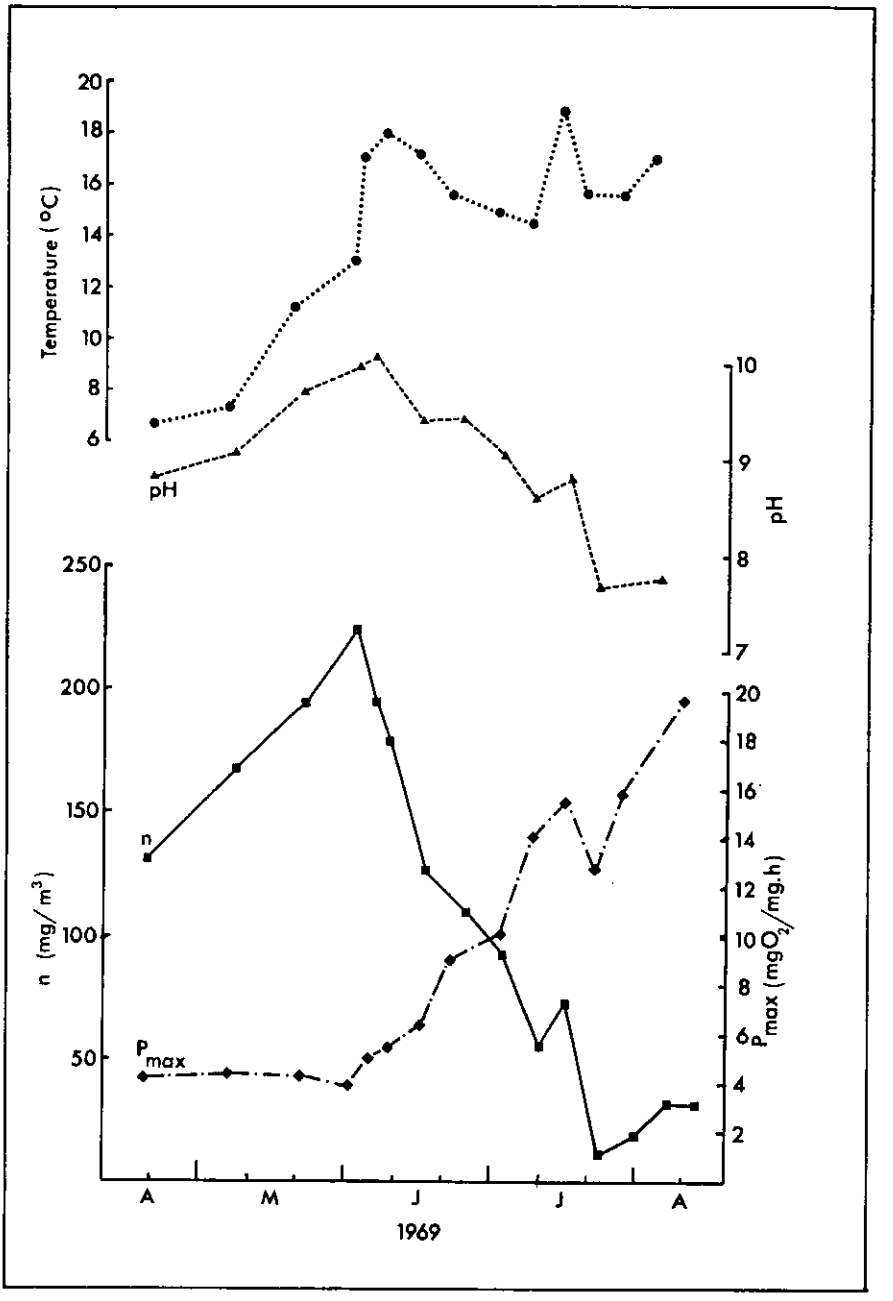


FIG. 11—Changes in population density (n) as mg chlorophyll a per m^3, light-saturated rates of photosynthesis per mg chlorophyll a (P_{max}), *p*H and temperature for the period April to August, 1969.

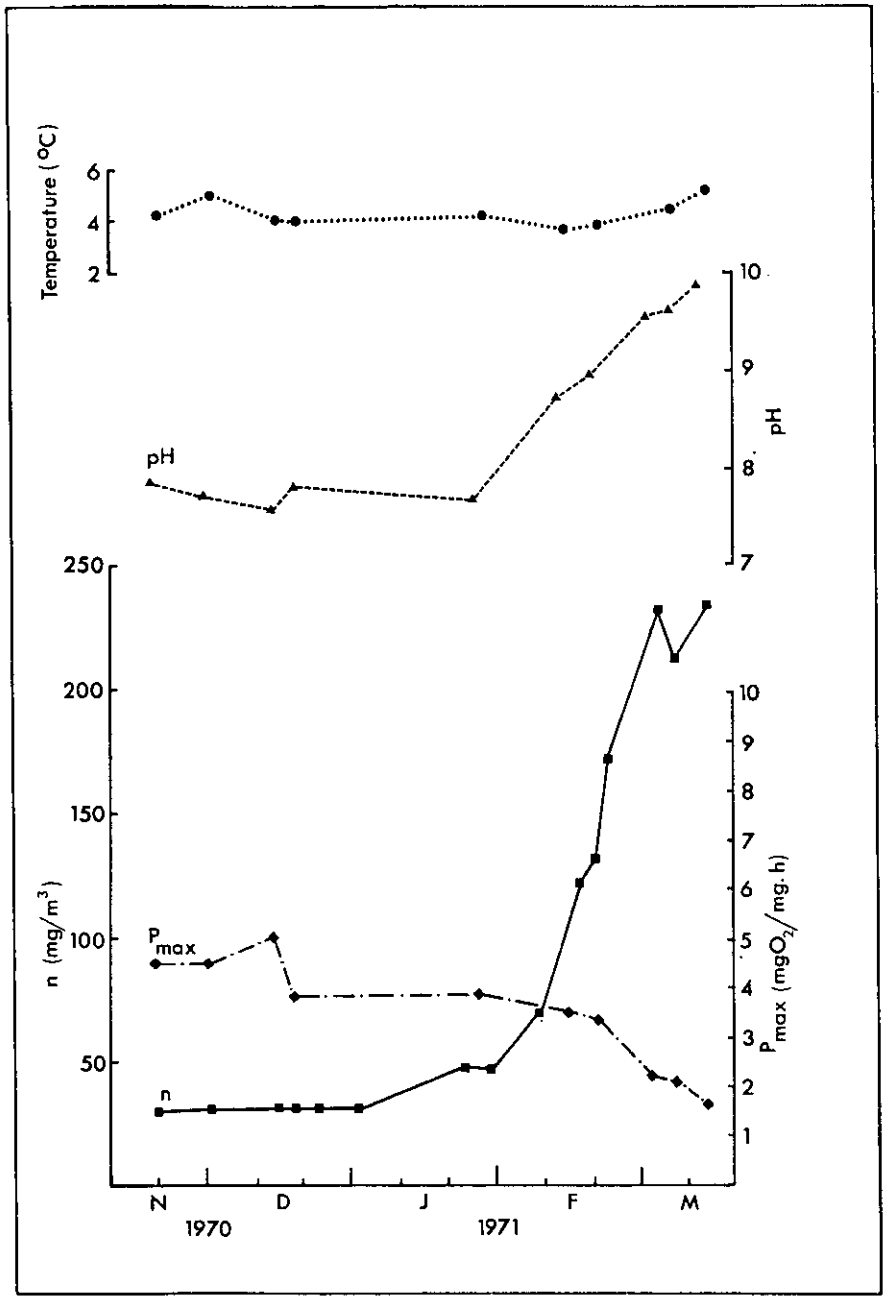


FIG. 12—Changes in population density (n) as mg chlorophyll a per m^3, light-saturated rates of photosynthesis per mg chlorophyll a (P_{max}), *p*H and temperature for the period November 1970 to March 1971.

The results of five experiments are summarised in Fig. 13. A trend of increase in capacity with reduction in *p*H from 9·8 to 8·0 is repeated in each experiment. (Maximum increase is 78 per cent.) When the *p*H is reduced below 8·0 the percentage increase in capacity is much reduced. When *p*H was increased on 19 March 1971 from 9·30 to 9·80 and 10·25 (by addition of NaOH) capacity was reduced.

These results suggest that the high *p*H values produced by photosynthesis in dense crops may inhibit P_{max}, i.e. photosynthesis may be self-limiting.

Possible explanations for the effect of *p*H on P_{max} include:

(*a*) reduction in availability of free CO_2 with increase in *p*H.

(*b*) reduction in phosphate uptake at high *p*H values.

(*c*) a direct effect of *p*H on cell membrane permeability.

Nitrogen and phosphorus supply

Laboratory experiments were carried out in order to detect possible nutrient limitation of primary productivity at different times of year. Effects of enrichment with N, P or N plus P on crop density measured as chlorophyll a

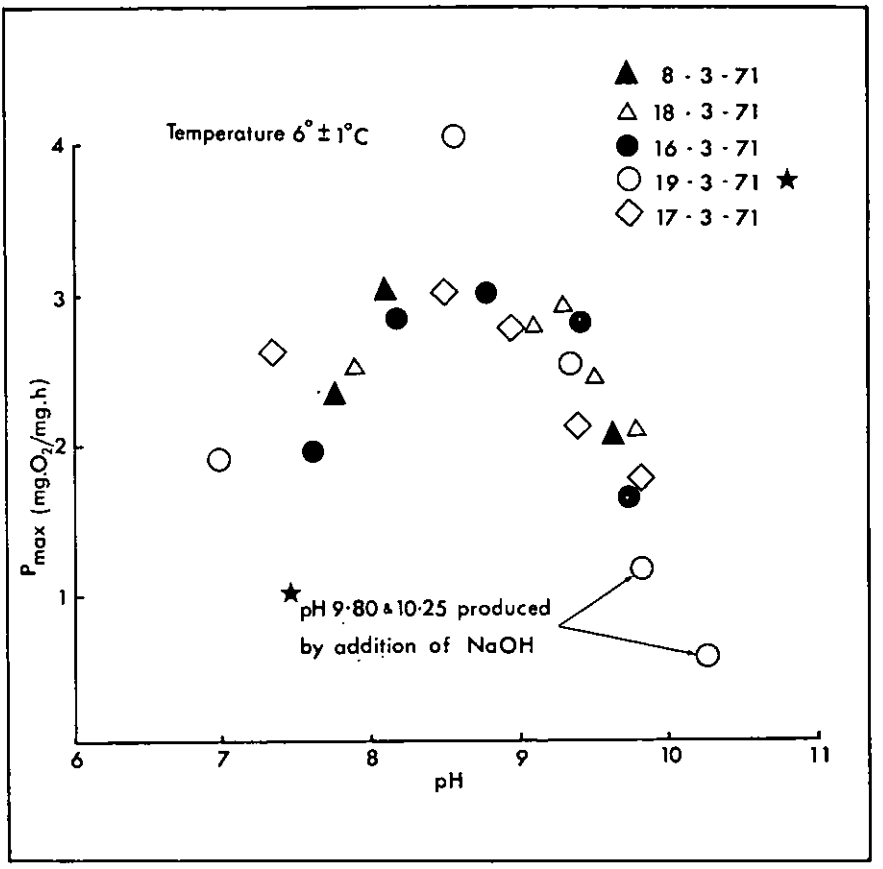


FIG. 13—Results of five experiments on the effect of lowering *p*H (by CO^2 in lung air) or increasing *p*H for two points only on 19 March 1971 on light-saturated rate of photosynthesis per mg chlorophyll a (P_{max}).

and on photosynthetic and respiratory rates were detected after growth in Erlenmeyer flasks, in continuous fluorescent light (750 foot candles) for 18 or 42 h. Results for the period June–September 1970 are shown in Table 7. During subsequent months it proved difficult to maintain temperatures in the laboratory low enough to approximate to lake temperatures. Therefore this type of experiment was discontinued but will be resumed now that an illuminated growth cabinet capable of operation down to 5°C has been obtained.

As compared with the 'light-grown' control the effects of nutrient enrichment are:

(*a*) In terms of chlorophyll content, phosphorus alone has no effect; nitrogen alone is stimulatory; nitrogen plus phosphorus is more stimulatory than nitrogen alone.

(*b*) In terms of photosynthetic capacity, effects are less 'dramatic' and less consistent but again in general phosphorus alone is less stimulatory than nitrogen alone. Nitrogen plus phosphorus on two occasions was more stimulatory than nitrogen alone.

It is debatable, however, whether the stimulatory effect of nitrogen plus phosphorus is indicative of their deficiency in the loch because by transferring the sample from loch to flask we are separating it from its supply of nutrients from inflow and bacterial recycling in sediments. At best the results can only indicate which nutrients are potentially limiting if their supply from inflow and sediments is cut off.

Another point which complicates interpretation of the results is that whilst nitrogen plus phosphorus seems to enhance photosynthetic capacity over the light-grown control, this apparently enhanced capacity is never higher than the original capacity of the material (values not shown in Table 7) before it is placed on the lights. Further, when a dark-control is included, the light-control material shows reduced photosynthetic capacity as compared with the original whereas the dark-control retains the capacity of the original sample. The decline in photosynthetic capacity in the light is reduced in the presence of added nitrogen and phosphorus.

Because of the uncertainties of the use of a nutrient enrichment technique for detection of nutrient limitation, other methods are being investigated. For example, the measurement of enzyme activities such as alkaline phosphatase and nitrate reductase may be used as indicators of the nutritional status of the population and may reflect its 'nutrient history'.

(*M. E. Bindloss*)

5. Benthic Invertebrate Fauna at Loch Leven

(a) *Shallow water*

Research on the shallow water benthos in Loch Leven started in August 1967, the main aim being to determine the annual production of the dominant species there, especially those important in the food chain leading from algae to fish and diving duck. The shallow water benthos of Loch Leven is essentially that found in sand, which occupies about 45 per cent. of the loch bed. Other substrates in shallow water (stones and weed) are insignificant in their extent and cover only about 1 per cent. of the loch bed. The initial phase of the project (up to 1970) has mainly involved studies of methodology, taxonomy,

TABLE 7. Effect of nutrient enrichment on chlorophyll a content (n) as mg/m^3 and photosynthetic capacity (P_{max}) as mgO_2/mg chlorophyll a. h of phytoplankton incubated in continuous fluorescent light or in darkness

Date in 1970	Incubation period (h)	n Nutrients Added N	n Nutrients Added P	n Nutrients Added N+P	n Control Light	n Control Dark	P_{max} Nutrients Added N	P_{max} Nutrients Added P	P_{max} Nutrients Added N+P	P_{max} Control Light	P_{max} Control Dark
19 June	90	116	45	436	55	—	2·5	4·1	2·7	3·5	—
25 June	18	172	126	172	118	—	3·3	3·4	3·6	3·3	—
25 June	42	—	—	226	87	—	—	—	3·7	1·6	—
29 June	41	133	50	183	60	—	2·9	2·3	5·6	1·8	—
21 July	18	57	36	63	35	—	6·0	4·5	6·4	3·8	—
21 July	42	63	21	143	23	35	5·6	3·3	5·7	3·4	—
14 August	18	115	61	126	57	84	5·3	5·2	7·0	5·1	9·1
14 August	42	129	42	288	42	67	3·5	3·5	4·0	3·0	9·2
27 August	18	—	—	144	110	119	—	—	6·0	4·0	11·0

biology and the feasibility of measuring the production of the main components of the benthos. During 1970 and 1971 production measurements over the whole of the sand area are being carried out, and these will be processed and written up during 1972.

One of the initial problems in sampling the sand was that, unlike the mud where several suitable samplers were available (see below), no suitable quantitative sampler was available and some time and effort was spent in developing a corer suitable for this purpose. This has been fully described elsewhere (Maitland, *Limnol. Oceanogr.*, **14**, 151–156). An initial series of cores from the sand showed that almost the entire fauna of this substrate is made up of Nematoda, Oligochaeta, Diptera and Bivalvia. Comparative hand-net collections from sand, stones and weed indicate that the latter two types have a more diverse fauna including various species of Gastropoda, Ostracoda and other Crustacea.

Thirty cores were taken at different times and places in the sandy area of the loch to investigate the vertical distribution of the fauna there. All were 7 cm diameter cores 15 cm in depth and each was sectioned horizontally into three parts. The results for the full series are in Table 8. There was no evidence of size differences among animals of the same species found at different depths.

TABLE 8. The vertical distribution of invertebrates in 30 cores of mean diameter taken at random from the sand area.

Fauna	*Total no. collected*	*Occurrence in sediment as percentage of total*		
		0–5 cm	*5–10 cm*	*10–15 cm*
Nematoda	4,602	63	30	7
Oligochaeta	2,157	87	9	4
Mollusca				
Valvata	10	90	10	0
Pisidium	105	98	2	0
Diptera				
Glyptotendipes	214	97	2	1
Stictochironomus	445	94	5	1
Endochironomus	17	100	0	0
Tanytarsus	517	96	3	1
Others	378	96	3	1
Total	8,445	91	7	2

Cores taken from the loch bed are subjected to washing to separate the fauna from the remainder of the substrate. They are first fixed in 4 per cent. formaldehyde and each core is left for 48 h to allow the animals to harden. The washing method is a simple decantation one, based on differences in specific gravity between the invertebrates (even Mollusca) and sand grains. The fluid in each sample is decanted into sieves. Water is then run into the sample vigorously so that all the sand is disturbed; as soon as it has settled the water is decanted again. This process is repeated four times. The method was tested by trials involving two sets each of 30 cores—each core being decanted ten times and the numbers of animals coming off at each decantation sorted from organic debris and counted. The remaining sand was then

examined for any remaining animals. Table 9 shows that five decantations for each sample results in virtually 100 per cent. separation.

TABLE 9. The numbers of four common invertebrates in successive decantation from two sets (A and B), each of 30 cores.

		Decantation										*No. left in*
Fauna	*Set*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*sand*
Glyptotendipes	A	4	7	3	3	1	0	0	0	0	0	0
	B	109	259	43	20	6	1	1	0	0	0	0
Stictochironomus	A	274	187	10	0	0	0	0	0	0	0	0
	B	71	69	2	0	0	0	0	0	0	0	0
Cryptochironomus	A	2	3	0	0	0	0	0	0	0	0	0
	B	26	15	3	0	0	0	0	0	0	0	0
Pisidium	A	8	25	6	3	1	0	0	0	0	0	0
	B	9	16	7	7	6	2	1	0	0	0	0

Preliminary evidence showed that many of the major species of invertebrates in Loch Leven are confined to specific substrate types. In order to investigate this so that the loch could be divided into meaningful zones for sampling purposes, a survey of the sediments and their associated benthos was carried out in October 1968. Three cores were taken at each of more than 100 stations spread evenly over the whole area of the loch. Graphical analyses and more complex correlation analyses by computer indicated that the major distinction among the sediments lies between sand and mud, and that there are fundamental differences between the benthic communities associated with these types. There are considerably more variations in the type of species and the numbers found within the shallow water sand area than within the deep water mud area. The present survey indicates three major types of community within the sand area.

Table 10 gives an example of the relationship between sediment type and the occurrence of certain species of invertebrate. *Stictochironomus* (one of the common midge species in the loch), for example, is clearly restricted to substrates characterised by a low percentage loss on ignition. Some of the causal relationships between such biological and physico-chemical parameters have been investigated in the field and in the laboratory. One of the most important of these in the shallow water area appears to be the effect of wave action.

TABLE 10. The occurrence of *Stictochironomus* in relation to the loss on ignition of the sediment at 85 stations

Percentage loss on ignition (dry weight)	0–0·5	0·6–1·0	1·1–1·5	1·6–3·0	3·1–5·0	5·1–10·0	10·1–15·0	15·1–30·0
No. of stations in each category	7	11	16	8	5	9	14	15
No. of stations with *Stictochironomus*	7	7	4	2	1	0	0	0
Percentage of stations with *Stictochironomus*	100	64	25	25	20	0	0	0

Work on the life cycles of major species of Chironomidae has shown that most of these are univoltine, though in some years part of the population may be bivoltine. It appears probable that the production of most species can be estimated using the graphical technique developed by Allen (1951, *Fish. Bull. Wellington, N.Z.*, **10**, 1–231), providing the data on larval density and weight are known accurately enough. Preliminary estimates of the production of some common species at a few points in the loch have been made. Thus at one station in 1968 the total production of *Stictochironomus* larvae is estimated at 11·8 gm (dry weight) per m^2. From proportional relationships on the density of this species at 85 other stations in the loch the total production of these larvae in Loch Leven during 1968 is calculated to have been 41,300 kg (dry weight).

Based on the results of the methodology work described above, a full sampling programme for 1970 and 1971 was drawn up. The sand area was divided into three major zones and each of these is sampled at intervals at a number of points in each zone, previously determined on a random basis. In parallel with this sampling, some independent measurements of growth have been obtained (by isolating larvae in special chambers in the loch), and regular collections of adults have been taken to provide additional data on the life cycles and taxonomy of the species of Chironomidae involved.

Stomach contents of trout, perch and tufted duck from Loch Leven were analysed in order to determine the role of various benthic invertebrates in their diets. The results (Table 11) showed that larval and pupal Chironomidae formed a major part of the food of fish and duck at all times of the year.

TABLE 11. The food eaten by tufted duck (*Aythya fuligula*), trout (*Salmo trutta*) and perch (*Perca fluviatilis*) at Loch Leven

	Average percentage composition by bulk of stomach contents examined		
Food items	*Tufted duck*	*Trout*	*Perch*
Plant material	25	0	0
Oligochaeta	0	1	3
Crustacea	3	7	37
Diptera	51	55	49
Trichoptera	10	1	1
Mollusca	8	14	0
Others	3	11	10
Aerial	0	11	0

(*P. S. Maitland, Miss P. M. G. Hudspith*)

(b) *Deep (>3 m) water*

The aim of this study is to measure the annual production of chironomid larvae and pupae in the mud, to relate these findings to other work on their metabolism and feeding, and thus measure energy flow from algae to the tertiary producers.

The mud on the bed of the loch is a deep layer which is only rarely deficient in oxygen due to the thorough mixing of the water. Chironomidae are the commonest secondary producers in the zone; they also form the largest

component in the food of fish (60 per cent. by bulk from a series of samples taken in 1968).

The study has progressed through three phases. Qualitative surveys were initially done to determine the overall composition of the benthic community and later the composition, general abundance, distribution, movement and the seasonal life cycles of the common chironomids. During 1968–70, the work centred on developing quantitative methods for estimating production, and these were tested in study areas covering 10 per cent. of the mud zone in 1970. During 1971 production of larvae is being measured within the zone excluding two small areas in which the depth exceeds ten metres.

Surveys conducted in 1967–68 showed that eight genera—*Chironomus*, *Glyptotendipes*, *Limnochironomus*, *Polypedilum*, *Cryptochironomus*, *Tanytarsus*, *Pentaneura*, and *Procladius*—were common within the area (500–50,000/m^2). *Chironomus* and *Tanytarsus* were evenly distributed, except that the latter was absent from the deeps, while the numbers of *Glyptotendipes* and *Cryptochironomus* were more variable and possibly associated with the proximity of sandy areas. Two genera at least (*Chironomus* and *Procladius*) were represented by more than one species, each with a different life cycle. Most of the larger species were univoltine, but *Glyptotendipes* had a partial second generation in some years, *Tanytarsus* was bivoltine and *Procladius* multivoltine. There was also evidence to suggest that some species immigrated into the mud from the sand zone at certain times of the year.

The investigation into methods had two objectives, (*a*) to determine how to measure standing crops and growth rates within given confidence intervals and (*b*) to speed up sampling and sorting so that the programme could eventually cover the whole mud zone. During 1966–68 four series of trials were conducted with an F.B.A. corer, Jenkin corer and Ekman grab to see which was the most efficient sampler to use in the mud of this loch. On each occasion the catch from the Jenkin corer was significantly higher than from the others (at the 5 per cent. significance level on three occasions and between the 5 and 10 per cent. level once). The Jenkin corer was therefore chosen for this study.

The vertical distribution of larvae in the mud was measured to see how far the sampler should penetrate (Table 12). Almost all the larvae found below 15 cm were large *C. plumosus*. (These have decreased in numbers since this investigation.) As a result of these trials the samplers were adjusted to take 20 cm cores. During 1969 the corer was calibrated against independent measurements of standing crop to check its true performance. Using divers, 0·5 m^2 quadrats of mud were enclosed to a depth of 25 cm, pumped up to the surface, subsampled and sorted. These counts were compared with those from a series of Jenkin cores taken in the immediate vicinity. The estimates of numbers and biomass from the two series of samples were found to be similar.

Prior to planning a sampling scheme for measuring the mean standing crop of larvae within a stratum, it was necessary to know their dispersion characteristics in space and time. This would provide information from which predictions could be made about the degree of variation in counts from individual cores, and therefore, taking into account the density of each genus, the numbers and pattern of cores required to give estimates of mean standing crop within predetermined confidence intervals. The dispersion of larval populations was measured at two levels. Variations about a point were assessed

TABLE 12. The vertical distribution of chironomid larvae in the mud. The number and biomass of larvae present in 5 cm sections expressed as a percentage of the total from three Jenkin Cores taken at one point from April–December 1968

	April		*June*		*August*		*October*		*December*	
Depth (cm)	*Numbers*	*Biomass*	*Numbers*	*Biomass*	*Numbers*	*Biomass*	*Numbers*	*Biomass*	*Numbers*	*Biomass*
0–5	87·2	16·8	87·7	14·5	95·4	32·4	93·4	19·1	94·8	16·4
5–10	3·5	12·1	4·2	22·9	2·6	32·7	5·1	25·2	3·9	47·1
10–15	5·8	67·0	3·4	35·5	0·7	0	0·9	24·0	0·7	13·7
15–20	3·5	4·1	4·6	27·1	1·3	34·9	0·6	31·6	0·5	22·8

by comparing counts from cores taken around the calibration boxes. Patterns of 50 Jenkin cores from three areas of 12·5 ha were used to measure the variation on a larger scale. By combining these data it was possible to calculate the index of dispersion for each genus and the degree to which the small- and large-scale components contributed to the total. The time available to pursue this problem was limited and the results could only be treated as rough indicators, but it appeared that the degree and scale of clumping differed between genera. For example, *Procladius* showed marked variation about a point, while in *Chironomus* numbers varied on a larger scale. Table 13 shows the estimated number of individual cores required to estimate mean standing crop in six genera with confidence intervals varying from ±5 to ±30 per cent. Because of the differences between genera one pattern of cores could not be equally efficient for each type of larva; the system evolved for this study utilised a series of groups of cores sited randomly within each stratum.

TABLE 13. The number of Jenkin samples required with 95 per cent. certainty to give estimates of mean standing crop of larvae over an area of 12·5 ha in organic mud during July 1969, within confidence limit ranging from ±5 to ±30 per cent.

	Half width confidence intervals					
	0·05	*0·10*	*0·15*	*0·20*	*0·25*	*0·30*
Chironomus	645	160	70	40	25	18
Glyptotendipes	430	110	50	27	17	12
Tanytarsus	200	50	22	12	8	6
Limnochironomus	245	60	27	15	10	7
Polypedilum	261	65	29	16	10	7
Procladius	140	35	16	9	6	4

To overcome the problem of movement of larvae, independent measurements of growth rates were required. During 1969–70, undisturbed populations of larvae were enclosed within ventilated boxes sited on the mud and sampled at weekly intervals by divers using hand cores. In the earlier designs, the larvae suffered from an oxygen deficiency but after redesigning the pumps and system of circulation their performance was judged to be reasonably satisfactory. To save time and the inevitable small risks involved in diving, a new pneumatically powered grab was designed so that 0·25 sq m of undisturbed mud could be collected and brought to the surface. This permitted growth boxes to be established and sampled from the catamaran.

Although there was insufficient time to measure the production of adult chironomids, representative samples were required for taxonomic purposes. Existing designs of floating and submerged emergence traps were tried and found to be unsuited to the conditions at Loch Leven. Using samples collected by the pneumatic grab, a different design of trap will be used through 1971 which is expected to provide a limited number of quantitative samples.

Taxonomic studies have included the rearing of larvae from eggs and detailed examination of selected samples from Jenkin cores. *C. plumosus* and *C. anthracinus* can be identified as larvae but further work is needed if the three common species of *Procladius* are to be separated.

The most time-consuming aspect of this study has been the sorting of samples to give accurate counts and biomass measurements of all larvae from

first to fourth instar. The process has been mechanised as far as possible, and most of the instruments have been designed or modified for this study. These include mechanical sieves, large and small mechanical subsamplers, flotation tanks, rotating stages for microscopes, and modifications to a microbalance which together have reduced processing time by about 75 per cent. Trials conducted on sorting methods showed that losses during the separation of larvae were less than 5 per cent. Species, numbers and individual body weights are recorded and coded on to 80 column sheets for subsequent analysis.

During 1970, a sampling programme was completed within the mud zone using two trial areas, one of 20 ha and the second of 80 ha. The aim of this work was to test sampling methods developed over the previous two years. The results showed that confidence intervals on all estimates were close to those predicted. When measuring mean densities of larvae within a stratum, the precision of estimates for each genus ranged from ± 10 per cent. at the 95 per cent. level for the more abundant types of larvae to ± 30 per cent. in those where densities were relatively low. Mean body weights could be estimated with greater precision and confidence intervals here were usually less than ± 5 per cent. The relationship between these figures and confidence intervals for production estimates is now being examined, but it seems unlikely that they will exceed ± 25 per cent.

The composition of the larval community within the mud zone has varied from year to year and this process continued through 1970 within the study areas. *Tanytarsus* was almost absent; *Chironomus anthracinus* (averaging 2,500 larvae per sq m) replaced *C. plumosus* as the most abundant species within the genus; *Glyptotendipes* overwintered during 1969–70 in high numbers (av. 10,000/m²), but the next generation settled down to about 10 per cent. of this level between August and December; numerically *Procladius* spp. was the most important genus later in the year (av. 5,000/m²), and *Pentaneura* increased from earlier years (av. 700/m²); numbers of *Polypedilum* and *Limnochironomus* remained fairly static (av. 500/m²). Although not strictly comparable, estimates of biomass of the standing crop of larvae during May (mostly representing larvae produced during 1969) and December 1970 (Table 14) give an indication of the magnitude of change in production from year to year.

TABLE 14. Estimates of mean biomass of larvae from a 80 ha area sampled during 1970

	Biomass/m² in grams dry weight	
	May	*December*
Chironomus anthracinus	2·34	6·20
Glyptotendipes sp.	22·54	1·34
Limnochironomus sp.	0·13	0·29
Polypedilum sp.	1·75	0·40
Pentaneura sp.	0·02	0·03
Procladius spp.	0·25	0·91
Total	27·03	9·17

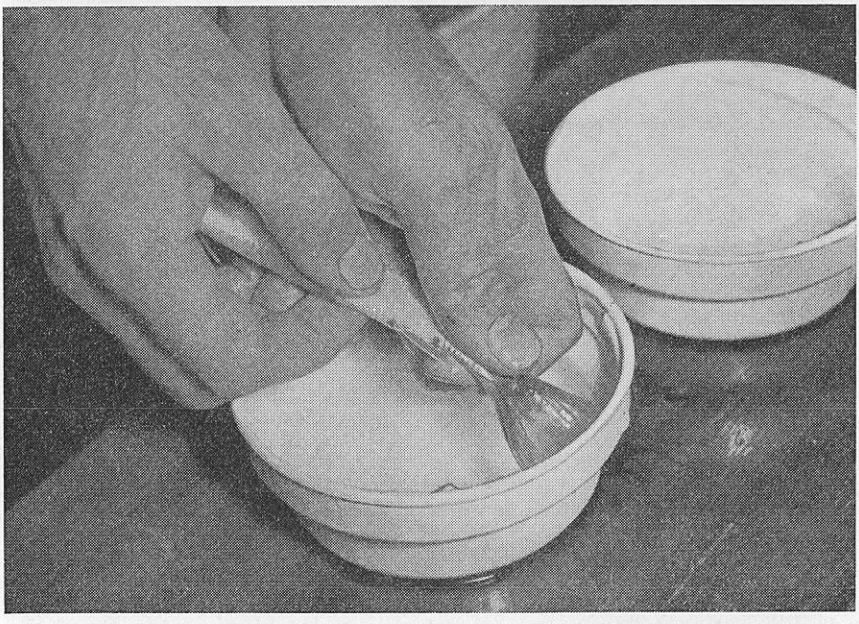
Although the larger of the two study areas ran from the western boundary of the sand zone to the centre of the mud, only small differences could be detected in the larval community across the stratum. The estimates of standing crop followed a consistent pattern through the year, and there was no evidence of any large-scale movement from other areas.

For the final year of field measurements, the mud has been divided into seven equal strata. Each is sampled by taking groups of randomly sited cores. 22 sets of samples will be taken through the year (about 5,000 cores) together with limited measurements of growth rates of larvae and emergence of adults. During this sampling certain other biological and physico-chemical parameters will be measured so that the analyses can also examine relationships between chironomid larvae and other components of the system. Such information should contribute towards the planning of future management-orientated research.

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

6. Conservation of Rare Fish Species

The recent scheme to map the distribution of all freshwater fish species in the British Isles, organised through the Biological Records Centre of the Nature Conservancy, has enabled us for the first time to have some idea of the present distribution and status of the 54 species concerned. Active steps are being taken to conserve one of our rarest forms, the Lochmaben vendace (*Coregonus vandesius*), at present known to occur in only one water in Scotland, the Mill Loch at Lochmaben in Dumfriesshire. It has disappeared from its former stronghold at the Castle Loch, Lochmaben due to pollution.



Artificially stripping eggs from a vendace.

The present scheme has involved the selection of three hill lochs in Galloway, thought to be suitable for the species and in which viable populations could be established. Controlled netting of the Mill Loch has been carried out in the early winters of 1968, 1969 and 1970. In 1968, 5,000 fertilised eggs were obtained and introduced to the lochs concerned. No eggs were obtained in 1969. In 1970, only about 400 fertilised eggs were obtained; these have been hatched in the Edinburgh laboratory and the fry placed in local ponds for rearing so that very large numbers of eggs may be available for stocking in 2–3 years' time. The project will terminate when breeding populations of vendace have become established in the Galloway lochs concerned.

(P. S. Maitland, K. East)

7. Peatlands

Over the past three years, work on peatlands has largely been devoted to a survey of bogs, fens and marshes throughout Britain, as part of the Conservancy's Conservation Review. Following this an inventory of all known peatland sites worthy of conservation has been compiled in order to give a conservation grading to these sites at both the national and regional level. In addition, an increasing amount of time has been spent in giving advice on various peatland conservation problems at the request of both regional staff and outside bodies. Detailed investigations of selected sites have now commenced as a basis for a descriptive account of British mire systems.

The object of the broad survey was to describe the field of variation of British mires so that representative sites could be recommended as suitable for designation as National Nature Reserves. Because of the short period available this survey was mainly restricted to mire vegetation. No attempt was made to investigate variations in hydrological regime or chemical status. Furthermore the absence of systematic recording of invertebrate groups from most of the important peatland sites (other than some of the fens) meant that this aspect of mire ecology could not be adequately considered. Wherever it was available, stratigraphical information was utilised in describing the field of variation.

Since the main object of the survey was to recommend the best examples of each major type of mire system, it was necessary to ensure as complete a coverage as possible. The survey therefore consisted of several phases. Existing information was collated from a variety of sources. Regional staff provided lists of all the sites considered to merit further examination and other sources of information included the Mires Research Group, university lecturers, museum staff, the Field Studies Council, amateur naturalists, published papers and the Biological Records Centre. It became evident that certain parts of the country were not adequately known (notably mid Wales, parts of northern England and much of Scotland) and in those areas important sites were identified by examining maps and aerial photographs followed by field survey. Special efforts were made in certain areas where particular types of mire are well developed, for example, the blanket mire of Sutherland, Lewis and Wigtownshire and the basin mires and blanket mires of the Scottish border counties.

Fig. 14 shows the distribution (by 10 km squares) of sites which have been examined during the Conservation Review. Fig. 15 indicates the distribution of peat in Britain. The apparent lack of cover in the Scottish

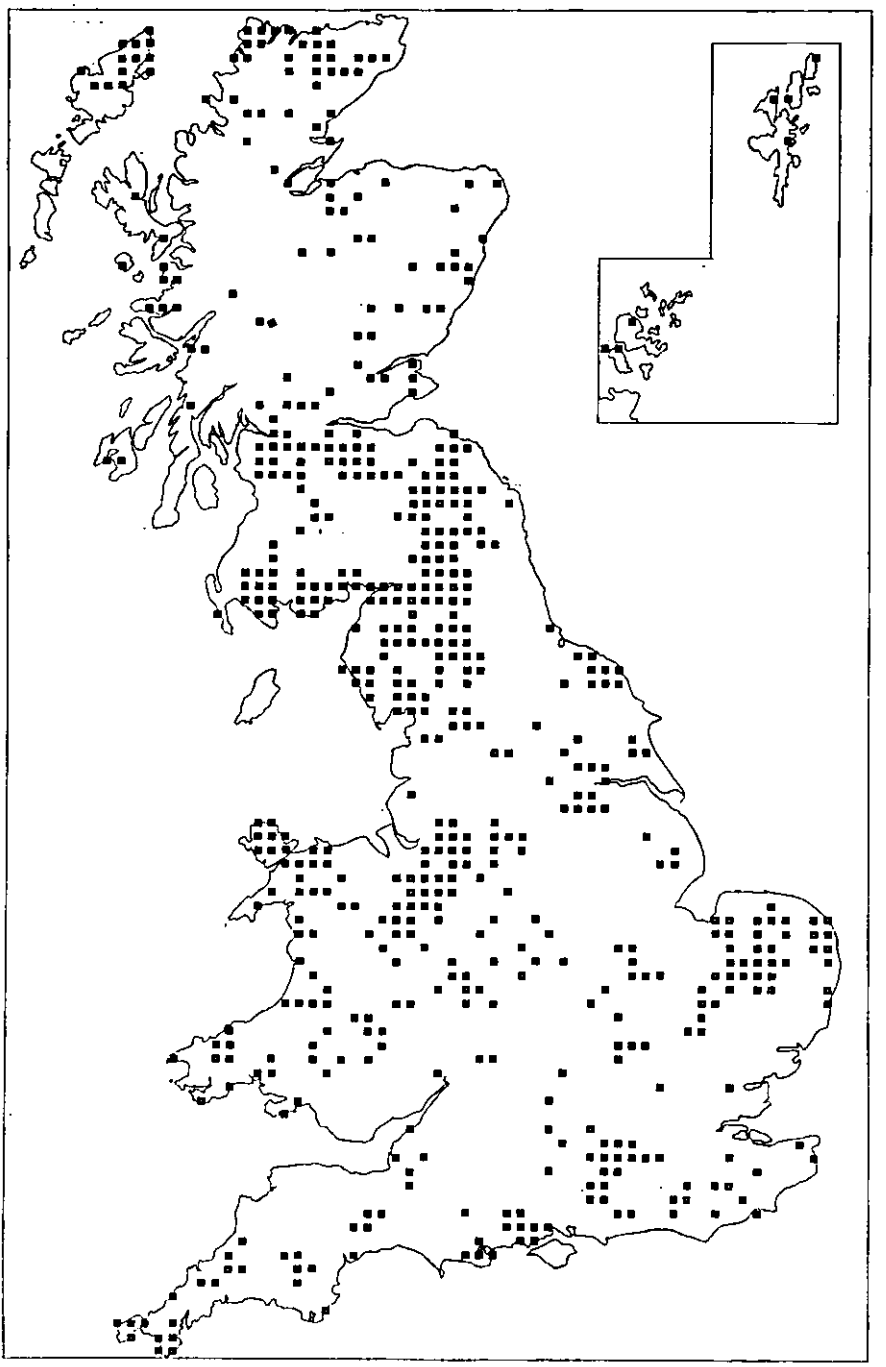


FIG. 14—Peatland sites examined during the Conservation Review. Map showing the distribution of sites examined (by 10 km squares).

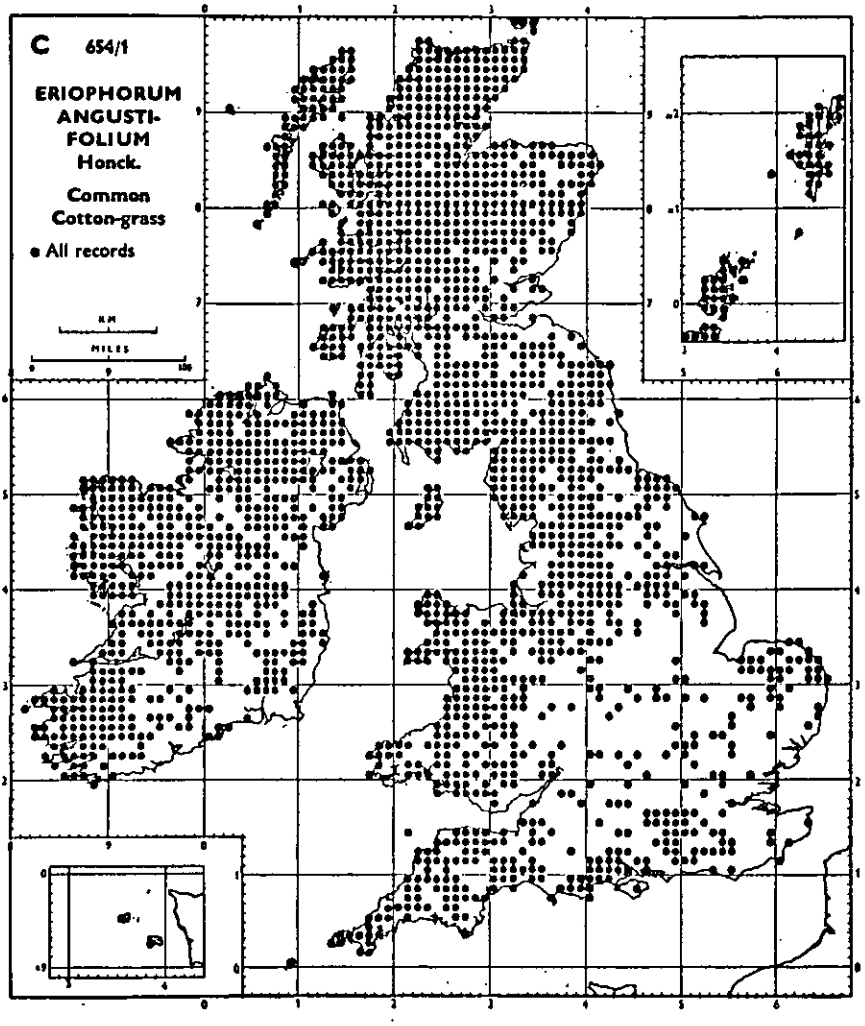


FIG. 15—Map showing the distribution of *Eriophorum angustifolium* which provides an indication of the distribution of peat in Britain. (By permission of the Botanical Society of the British Isles and Thomas Nelson & Sons Ltd, taken from their Atlas of the British Flora.)

Highlands is due to the fact that it was possible to select the most important sites from the survey of McVean & Ratcliffe (1962, *Plant Communities of the Scottish Highlands*), but parts of the western Highlands and Outer Hebrides are still not adequately examined.

Six major types of mire are recognised which are categorised according to the conditions responsible for their formation. These are valley mire, basin mire, flood-plain mire (inundation fen), upland soligenous mire, blanket mire and raised mire. This hydromorphological classification gives due emphasis to growth and structure of mire systems which is a fundamental feature of their scientific interest. Each major type shows a range of vegetational variation related to broad differences in climatic and edaphic conditions, and

sites were selected to represent the main variants exhibited by each mire type. Having defined these, the main criterion for selection was the extent to which individual sites were modified by man's activities. High quality sites were recognised by the intactness of the whole mire system, especially the hydrological régime. The presence of sensitive communities (and even individual rare species) such as bryophyte communities in calcareous fens, and dwarf shrub or lichen communities in upland blanket mire, was taken to indicate relatively undisturbed conditions. In this way, site quality was assessed from floristic data in addition to field investigation. The final list shows wide differences in quality between sites because even the best examples of certain important types of mire have been severely modified. This criterion does not of course apply to those important mire systems such as the Norfolk Broads which actually originated due to man's activities.

Advisory work has largely been concerned with evaluating the conservation importance of sites threatened by development, or assessing the impact of such development. Examples are the effect of peripheral drainage on fen systems, and the extent to which peat cutting is likely to affect adjacent raised mire vegetation. Several training sessions in evaluating the conservation importance of peatland habitats were organised for regional staff, and a scheme was organised in conjunction with the Peak Park Warden Service for mapping the vegetation of the Kinder and Bleaklow area of the Peak District National Park.

(D. A. Goode)

8. Survey of British Open-Water Habitats

Open waters comprising fresh and brackish water lakes, ponds, pools, rivers and streams are certainly the most widespread of the natural or semi-natural habitats remaining in Britain. Conservation interests in open-waters are increasingly being threatened by water based recreational activities, water abstraction, river regulation and drainage, hydro-electric schemes and a variety of pollutional hazards including eutrophication, all of which may adversely affect wildlife. These threats are only partially offset by the creation of new open-water habitats in the form of reservoirs and gravel pits. Hence the urgent need for the survey and description of intact open-water sites in Britain, and the selection from the sites covered of a series of potential nature reserves which will adequately represent the complete range of variation of open-water habitat in Britain.

Such a survey has been carried out over the past three years as part of the Conservancy's Conservation Review, but in view of the enormous number of sites yet to be covered this survey will continue to be a function of the Wetlands Research Group, on a reduced scale, for several years to come. The survey was organised as follows: firstly, regionally based staff were asked to complete habitat cards giving geographical, physiographic and some biological details on as many sites in their region as possible. Analysis of the cards allowed the sites to be grouped into broad physical categories, e.g. large deep upland oligotrophic lakes, small shallow eutrophic ponds, etc., and also allowed some preliminary elimination of obviously non-intact sites, e.g. lakes receiving the effluent from large towns, or hydro-electric reservoirs. A further degree of selection was then required on the basis of the habitat card information to select sites on which a fuller biological survey was to be carried out. In

this initial selection the criteria used were the degree to which sites were intact and the degree of representation of the physical category of waterbody to which the site belonged. In the case of a large deep oligotrophic lake, for instance, an intact site should be one whose catchment is substantially free from human inhabitation or cultivation, and to be representative of this type of lake the shoreline should consist mainly of an inorganic substrate (sand, stones, boulders) and be free from emergent vegetation, and the water should be clear. In the case of lowland eutrophic lakes, the degree of 'intactness' necessary is less demanding and the criteria for representativeness are entirely different. A total of 267 sites were thus selected for biological survey (Fig. 16), and sufficient information was available in the literature on a further 19 sites which enabled their evaluation without the need for a survey.

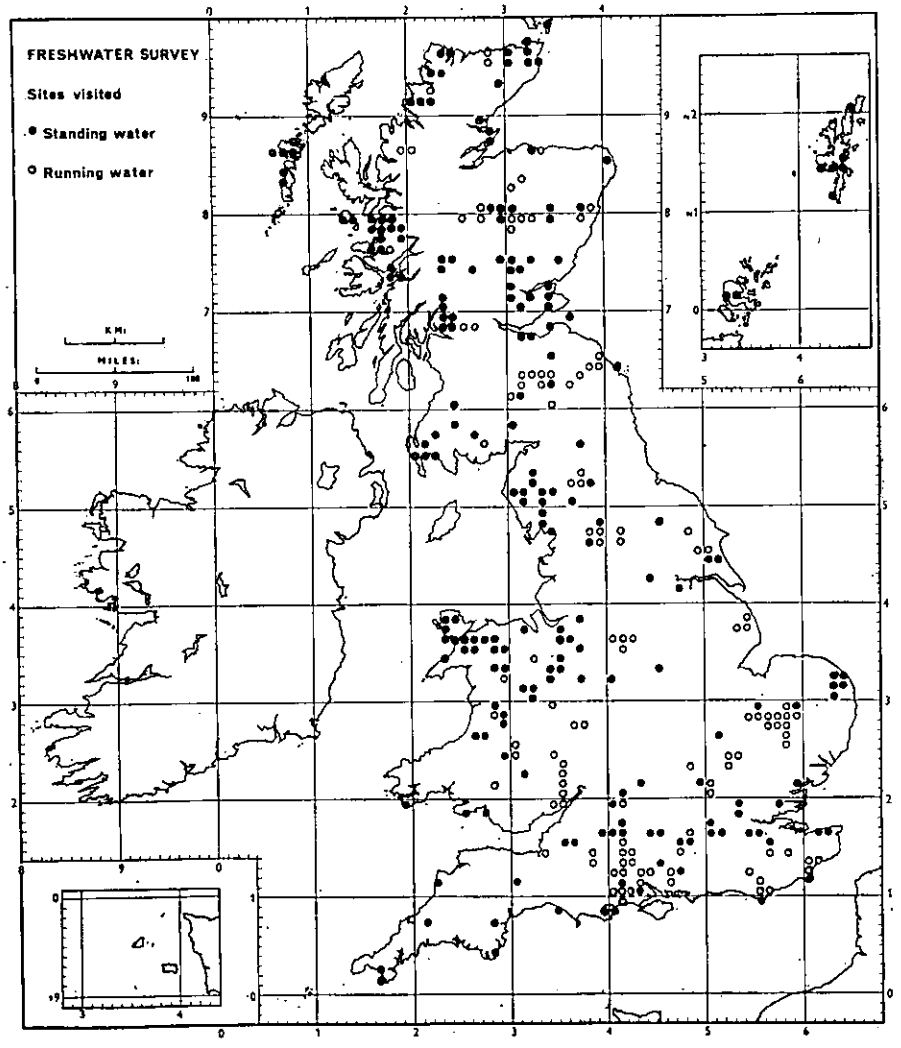


FIG. 16—Open water sites examined during the Conservation Review.

In the Conservation Review of other habitats, vegetational characters alone have often been used in describing and classifying the various sites, but this was not appropriate for open waters for the following reasons: (*a*) Aquatic plant communities have been little worked and the habitat requirements for most species are unknown. (*b*) It is difficult to obtain reliable estimates of the relative abundance of the various species of submerged plants. (*c*) Vegetation is sparse or absent in some sites of great conservation value. By contrast, the habitat requirements of many aquatic invertebrates are reasonably well known. Accordingly, although vegetational characters were taken into account in assessing sites, equal emphasis and a great deal more effort was put into faunal characteristics. Benthic invertebrates were collected using a combination of standardised hand net collections, dredges and Ekman grab samples, and a timed zooplankton tow was taken. Chemical characters were also used in assessing and classifying sites, and water samples were taken for the analysis of major inorganic ions by the Chemical Services Section at Merlewood Research Station.

The process of selecting the final series of top grade aquatic sites depends on establishing a sound classification of habitat types. Initially the classification is based on physico-chemical variables, but when the sorting and identification of the benthos samples is complete, this classification will correlate with a classification based on an association analysis of the invertebrate records. The initial separation in the classification is into running waters and standing waters. Within the standing waters, the next divisions are based on (*a*) alkalinity, which divides the lakes into oligotrophic, mesotrophic and eutrophic categories, and (*b*) specific conductivity, which differentiates lakes into dystrophic, brackish or marl. Dystrophic water bodies are distinguished by having a low alkalinity but a high conductivity due to presence of dissolved organic acids; brackish lakes are distinguished by their exceptionally high conductivity; and marl lakes by their high alkalinity in relation to conductivity. The next division is into type of shoreline. There are eight possible categories ranging from bedrock to a purely mud or peat shoreline. However, the shores of some lakes are so varied that more than one shore type predominates and different parts of the lake must be assigned to different categories. The final division is on depth, separating deep lakes (>5 m mean depth), which are likely to experience thermal stratification in the summer months, from shallow water bodies (mean depth <5 m) in which no stable thermal stratification is likely and in which the photic zone occupies most of the volume of the lake. On such a classification there are thus theoretically 96 possible types of standing water. These could be further subdivided in terms of area, altitude, vegetational cover, chemistry, period of ice cover and so on. In practice, however, the range, in Britain at least, is far more limited since the various factors are to some extent interrelated. For instance, oligotrophic lakes tend to be deep and to have rocky shores. In the case of running waters, fewer categories were chosen, the most important being chemistry, whether the stream was a depositing or an eroding one, the size of the stream and its altitude. Various parts of the same river could of course belong to different categories.

Having established a classificatory system the evaluation of sites is based on the following criteria:

(*a*) 'Intactness.' Natural waterbodies scored higher on this count than artificial waterbodies, the latter usually only being included where no

comparable natural alternative existed, e.g. Norfolk Broads. Any human interference with a site which was likely to affect the flora and fauna counted against the site on this score, e.g. eutrophication, water level regulation, etc.

(*b*) Representativeness. Each site was chosen as an example of a particular physico-chemical type of lake. The biota of a high grade site should contain only those species characteristic of the physico-chemical conditions of that type of waterbody. The more eutrophic a waterbody, the more highly its diversity was scored, both in flora and fauna and in numbers of microhabitats. In oligotrophic situations, on the other hand, uniformity of habitat and sparseness of flora and fauna, restricted to a few specialised groups, could score highly. In brackish situations grading to freshwater, a wide range of salinities and associated biota are desirable.

(*c*) Regional representation. In order to include species of restricted distribution in Britain, it was sometimes necessary to choose lakes of similar classification from widely separated geographical regions. Also, examples of distinct regional types of lakes, e.g. Breckland meres and the brackish lochs of the Outer Hebrides were included.

(*d*) Rare species. The occurrence of rare and especially endangered endemic species within an area added to its score, but was not sufficient to give a high grading to a site which was unsatisfactory on other criteria.

(*e*) Research. Some sites were chosen principally on the grounds of their interest as sites of prolonged past scientific research, though in this case the waterbody still had to satisfy the criterion of representativeness. In these cases, complete intactness was not necessary and nutrient enriched lakes such as Loch Leven were included.

The high-grade sites will be put forward for inclusion in the Conservancy's series of National Nature Reserves.

(*R. H. Britton, N. C. Morgan*)

Assistant Director's Laboratory

D. Jenkins

1. Introduction

Some projects on predator/prey relationships and the conservation of waterfowl were tackled from 1966. The first of these was on crows in Deeside by N. Picozzi. Despite long-term studies by A. Watson on golden eagles (and earlier work, now discontinued, by J. D. Lockie on mustelids), work on vertebrate predators had not been a major item in the Nature Conservancy's Scottish programme. This was a gap in our understanding of Scottish ecology, particularly since a lot of work has been done on prey species on which the impact of predation is imperfectly understood. Moreover, by British standards Scotland has a good predator fauna but the factors controlling their numbers and distribution are not well understood. At the same time, work was started by H. Boyd, assisted by C. R. G. Campbell of the Wildfowl Trust, on waterfowl with the aims of tackling conservation problems too distant from Slimbridge to be done by the Wildfowl Trust, and D. Jenkins exploited an opportunity to get good data on shelduck population dynamics on a local County Nature Reserve. Additional work on waterfowl is done by conservation staff throughout Scotland, and a typical project by a warden is reported by J. G. Young.

With the arrival of I. Newton in 1968, much of the waterfowl work started by H. Boyd was brought to a successful conclusion, except for limited aspects probably to be done by research students, thus freeing a scientist to work full-time with the small group interested in predators. No extra Conservancy staff had been available for this work; and the birth of the group was assisted through the excellent co-operation of the Royal Society for the Protection of Birds who asked D. N. Weir of their Aviemore group to work with N. Picozzi on buzzards in Speyside under D. Jenkins' direction. D. N. Weir had previously worked for several years on raptors in the same area. Now that R. Hewson is joining the D.A.F.S. to work on foxes, while remaining posted at Banchory, the group is further strengthened by a mammalogist, and due to this inter-departmental liaison the Predator Research Group has become a reality.

The Assistant Director was also responsible for supervising research students at Aberdeen University and, jointly with J. D. Lockie, at Edinburgh University. G. W. Johnstone and P. S. Bramley completed their theses at Aberdeen on the ecology and social behaviour of black grouse and roe deer in 1969 and 1970; and I. Colquhoun and P. W. B. Joslin are currently working on problems of range ecology and on the ecology and conservation of lions in India. All these student projects have been closely related to central problems tackled by Conservancy staff, even predation problems with lions (revolving around interactions between predators, their prey, and the range) giving a new insight into basically similar studies in Scotland as well as being important for conservation in India.

2. Research on Wildfowl

(a) *Wild geese in south east Scotland*

The Icelandic greylag geese (*Anser anser*) and pink-footed geese (*Anser*

brachyrhynchos), which winter annually in Scotland, each number more than 65,000 and feed entirely on farmland. This study started in 1967 and aimed to find what controls the distribution of these birds in south east Scotland and learn more of their feeding habits and crop-damage. Both species are distributed patchily, basing themselves on lakes and other water bodies on which they roost and from which they spread into surrounding land to feed. Pinkfeet prefer more secure sites for roosting, such as estuaries, large lakes and remote moorland pools, while greylag use mainly small lakes and rivers. Also, pinkfeet feed up to 30 km from their roosts, and greylag mainly within 3 km and at most 12 km. These differences in roosting and flighting habits tend to separate the two species spatially and reduce the extent to which they feed in the same places. Thus, of the total goose-country in south east Scotland, less than one-quarter is occupied by both species together, and the rest by one or other.

The two species eat almost every type of crop available on farmland, though neither selects food in proportion to its availability. Both eat grass throughout their stay, spilled grain mainly in autumn, old potatoes mainly in autumn, winter and early spring, and growing cereals mainly in late spring. The two species have similar diets but differ slightly in the proportions of various foods they eat. The greylag has the larger bill and eats more root-crops, turnips forming its main food at times of snow. The chief conflicts arise when greylag eat turnips in winter, and when both species eat young grass in spring. The main recommendations will be on how to manage farmland, so as to change the number of geese using it, on when to expect damage, and on how to minimise it.

(I. Newton, C. R. G. Campbell)

(b) *Greylag geese on Loch Druidibeg, Outer Hebrides*

The aims were to check the well-being of the native greylag breeding on the Hebrides and to study their interaction with the local agriculture, a source of complaint from crofters. Loch Druidibeg forms the main centre for the geese on the islands. In each of three years from 1968, 60–70 pairs nested on this loch, on scrub- or heather-covered islets, and 30–40 broods were raised, the remaining clutches being lost to crows and other predators. Also, about 250–300 non-breeding geese moult on the loch each year. Most of their feeding does not bring the geese into conflict with crofters, but occasionally the birds feed on re-seeded grassland or on growing cereals near the water's edge. The best remedies, as judged by a number of trials, are frequent disturbance, or the use of 'bangers' and scarecrows. The damage is sporadic and does not warrant controlling the geese, which are anyway shot in substantial numbers by the islanders each year.

(I. Newton)

(c) *Greylag geese in Galloway*

The aims were to investigate the biology of the feral population introduced to Lochinch near Stranraer, Wigtownshire about 1930, from eggs brought from the native colony on South Uist. By 1951 the geese were well established and had dispersed to breed up to 50 km from the original site. In 1971 the population was estimated at 900, breeding at 20 localities in four counties.

Most nests (87 per cent.) were on wooded islets, and only 1·2 per cent. failed through natural predation. Most eggs were laid in late March or early April, the incubation period averaged 29 days, and from 476 nests the clutches

ranged from 3–9 with a mean of 5·1. The hatching success was 87·6 per cent., there was no significant gosling mortality and the average brood in September was 4·0. The mean annual recruitment is estimated at 27 per cent.

Ringing gave a recovery rate of 18 per cent. and annual mortality was estimated at 25 per cent. The average distance moved each year was 20 km, and the stock was sedentary except for an annual moult movement between the Stranraer area and the higher hill lochs near Newton Stewart.

(J. G. Young, Warden, South Region)

(d) *Breeding ducks on Loch Leven, Kinross*

This project started in 1967, in conjunction with the Wildfowl Trust. Loch Leven is important because it holds one of the largest concentrations of breeding ducks in Europe, with 900–1,000 pairs nesting each year on a single island, mainly within 20 ha. Nine-tenths are mallard (*Anas platyrhynchos*) and tufted ducks (*A. fuligula*), in about equal numbers, and the rest include gadwall (*A. strepera*), wigeon (*A. penelope*), shoveller (*A. clypeata*) and a few others. Our chief interests were in the factors which promote such crowded nesting, important from a conservation viewpoint, and in studying those aspects of the breeding of ducks that would not be possible with the smaller samples available elsewhere. The ducks nest most densely in those types of cover in which they hatch their eggs most successfully. The main predators on the eggs are jackdaws (*Corvus monedula*) which nest on the island in holes, but human disturbance greatly influences the number of eggs they take. Over much of the island, about 45 per cent. of the clutches hatched each year, but in a control area, from which all people (including researchers) were banned till the end of the season, about 85 per cent. of the nests had hatched successfully, as shown by examining the old nests. The survival of ducklings on the loch is poor, apparently through lack of suitable cover in the right places. As a result of this study, several papers will be published shortly on the biology of ducks, and recommendations made for the management of the reserve. The project is now concluded except for some aspects to be taken up by a research student. *(I. Newton, C. R. G. Campbell)*

(e) *Population dynamics of shelducks* (Tadorna tadorna) *in East Lothian*

This spare-time project at Aberlady started in December 1966, and the birds' numbers have been remarkably constant from season to season in each of the last five years. This suggests that the shelducks may be a distinct local population and suitable for studying the processes involved in population control. The area is a local nature reserve with the spectacular shelducks providing a focus of interest. One problem is to find the proportion of the population that breeds each year, since an earlier worker at Aberdeen suggested that not all birds do so. Most of my conclusions depend on count totals and not on studies of known individuals, and I have done little work so far on food or behaviour.

All or nearly all full-grown shelducks leave Aberlady in July-August to moult elsewhere. They return to Aberlady from October onwards; this is earlier than at another neighbouring estuary. Nearly all full-grown shelducks seen at Aberlady are in adult plumage, with few first-year birds except in May–June; and the sex ratio of adults is about equal (with a few more drakes than ducks).

Maximum numbers have increased from about 50 in the 1950's to more than double in January–February now. In February or March, the wintering flock divides into two components. About 40 birds disperse along the nearby coasts, sometimes returning at high tide, while the remainder stay in the estuary. Up to late April when incubation starts, counts done on high tides usually show about 110–130 birds with about 70–90 at low tides. However, soon after dawn from late March, nearly all birds leave the Bay (and some leave the nearby coasts) for breeding areas, returning later in the day.

In 1969 and 1970, counts suggested that only about 20 pairs nested around Aberlady Bay, with some others going inland to nest, and others apparently not nesting. Few broods of ducklings are seen along the coast and inland, and in most years the total reproduction is poor—only nine young were reared in 1967; 36 in 1968, 123 in 1969, and 37 in 1970. Thus adult numbers remained stable although breeding success varied considerably.

The tentative conclusion is that regulation may be occurring at three levels: (*a*) the total which seldom exceeds 125; (*b*) the low tide population at about 70–90; (*c*) the apparent restriction on breeding around Aberlady Bay. The main purpose so far has been to obtain data on population changes and provide a good basis for more detailed work later.

(*D. Jenkins*)

3. Research on Vertebrate Predators

Predatory animals form an important part of our wildlife and countryside and arouse strong feelings among naturalists, sheep-farmers and game preservers. Moreover, biologists are often asked what exactly are the effects of predators on sheep and game stocks, and what are the relative effects of pesticides, sheep-farmers and game-keepers on predators? The projects described below fall within a general plan which is aimed to assess, in land under different uses, the densities of various predators, the factors limiting their numbers, and their relationships with their prey populations. They form a co-operative venture with the RSPB and the DAFS. So far all work by Conservancy staff has been with birds, but a student's project on lions in India is now being written up.

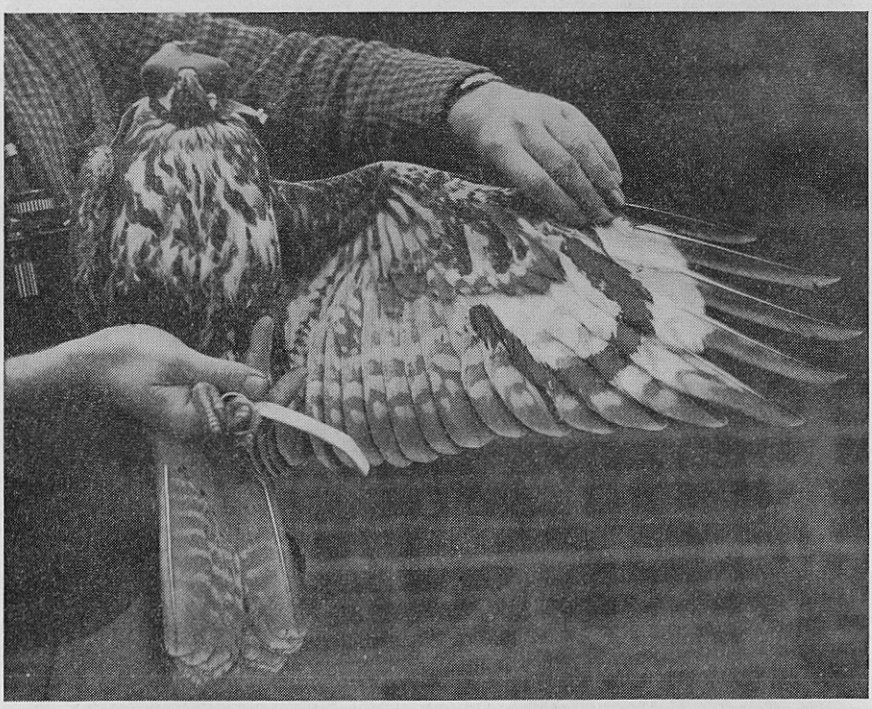
(a) *Crows* (Corvus corone) *on Kerloch Moor, Deeside*

This work began in 1966 aiming to study the breeding behaviour of crows and, in particular, to assess the effect of these birds on the nesting success of red grouse. Until 1966, the crows on Kerloch Moor were killed each year by the game-keeper, but the effectiveness of this control was not assessed. For three years from 1966, however, the crows were left alone, and then control was resumed for another three years from 1969. Each year the breeding success of the local grouse was measured, and it was hoped that a comparison between the two sets of years would indicate the importance of the crow as a predator of grouse eggs. The situation was complicated in 1967, however, by an experiment involving putting poultry eggs on the moor, and marking their positions with short bamboo canes 5 m away. It was intended to repeat this each year to give an index of crow predation under standard conditions. But the crows learned to associate the canes with eggs and not only removed the poultry eggs, but also most of the grouse clutches which had been marked in the same way. From 1968 the grouse nests were not marked.

Stopping shooting crows in 1966 made little difference to the number that attempted to breed in the 1,400 ha area. In this first year of respite, 19 pairs were present, and these had increased only to 23 pairs by 1969, when control was resumed. The control methods were a combination of shooting birds at the nest and the use of the narcotic alpha-chloralose in poultry eggs placed near the nests and on the moor. As a result, in 1969 and 1970, crows were almost eliminated and only one brood was fledged in the two years.

In the grouse, the ratios of young:old birds in the late summer of the first three years, when the crows were left, were 0·2:1, 0·3:1 and 0·7:1, and in the first two years of resumed control the ratio increased to 1·5:1 and 2·1:1. However, in the years when crows were left, the production of young by grouse whose nests were not robbed was also very poor, except on a very small fertilised plot (see above, p. 7). Hence, the three experimental years coincided with three years in which grouse breeding was poor anyway, so the results on the effects of leaving crows are inconclusive. So many factors influence the success of grouse each year that it is hard to design a satisfactory experiment to isolate the effect of crows alone, and this work has been discontinued.

(*N. Picozzi*)



Use of jess and dye for individual recognition of buzzards.

(b) *Buzzards* (Buteo buteo) *in Speyside*

This research started in 1969, with the aim of studying a population of buzzards to find the main factors limiting their numbers. Emphasis is placed on the role of 'territorial behaviour' in regulating density, for buzzards are numerous in the Spey Valley and easily watched. They are found only below

the 360 m contour, and 33–34 pairs nest in the 20,000 ha of the well-wooded study area. For two years, winter and summer, the territories have been mapped, as far as possible, by noting the movements of individual birds and the positions of boundary conflicts. With the help of a captive decoy, ten free-flying birds have been caught and marked so that they can be recognised in the field. In addition, details of nesting success and food have been collected from as many territories as possible, and many nestlings have been marked with metal and coloured rings. Not all the ground was occupied by breeding pairs, yet the territories remained roughly constant from winter to summer, and overlapped little, if at all, with their neighbours. From 33 pairs known in 1969, 29 built-up nests were found, but only 18 were later seen with eggs or young. The mean brood-size, determined from 15 nests, was 2·7. After fledging, the young were fed by their parents in their territories for varying periods up to mid October. Then, coinciding with increased territorial defence by the adults, the young dispersed, and most were not seen again. However, in the first year at least five young birds from elsewhere spent part of the winter in the study area, and in the second year at least one. These birds occupied territories of 40 ha or less, in the spaces between ground occupied by breeding pairs. The young disappeared in February–March each year, when a fresh movement of first-year birds occurred through the area.

Future work will include an attempt to relate territory-size and success both to the type of terrain and to the prey animals present.

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

(c) *Sparrowhawks* (Accipiter nisus) *in Dumfriesshire*

Although made scarce over most of Britain by toxic chemicals, sparrowhawks are still numerous in south west Scotland, where the arable acreage is small. In some parts of the area they can nest undisturbed, but in others they are still heavily persecuted by game-preservers, despite protective legislation. The emphasis of this study, which started in 1969, is placed initially on finding the density of breeding pairs and their success on keepered as opposed to unkeepered ground, and secondarily on assessing the impact of the hawks on their food-supply.

In each of two preliminary years, about 100 pairs are known to have been present in Dumfriesshire county in spring. More than half the woods visited at the start of the season held at least one pair of hawks, though many of these were shot in the ensuing weeks. The smallest wood holding a nest was only 2 ha in area. Woods up to 60 ha were usually occupied by only a single pair, but larger woods often held more. In 4,400 ha of an extensive forestry plantation 15 occupied nests were found, an average of one pair per 290 ha, with some nests only 500 m apart.

Of the 63 nests examined more than once, 38 were unsuccessful. In 12 of these the eggs failed to hatch; in three the hen disappeared and was probably killed by an owl (to judge from the feathers present); in 19 the hen was presumed shot (to judge from the holes in the nest); and four others failed through other human intervention. No instance of the eggs being eaten by a natural predator came to light, probably from the hen's habit of sitting on the nest during the laying period, as well as during incubation. Thus the major cause of failure was human interference in one form or another. Further, in the eggs which were incubated but failed to hatch, high pesticide levels were found.

The average brood-size in 25 successful nests was 2·6. Taking total failures into account, an average of one young per nest was raised to fledging.

Future work will include the second phase of the study, an assessment of the effect of the hawks on their food-supply.

(*J. G. Young, I. Newton*)

(d) *Hen harriers* (Circus cyaneus) *in Deeside*

Because hen harriers are one of the major predators on red grouse, on many moors they are killed at every opportunity, despite protective legislation. This study, started in 1970, is aimed to assess the impact of harriers on grouse stocks and involves detailed work on selected pairs.

It soon became obvious that harriers may hunt a long way from their nests, and the first problem was to find a way of marking the birds so that they could be recognised in the field. The birds could then be followed, their hunting areas found, and counts of prey made there. In 1970, six nests were found, but only two were successful, producing a total of eight young. These young were all marked with a numbered ring on one leg and a plastic jess on the other, and two of them were also given a patagial tag, as was an adult female caught at one of the nests. Two of the three birds marked with patagial tags were seen the following winter, showing that they survive this treatment, so further trials will be made.

Of the 64 prey-items so far found at nests, 28 (44 per cent.) were grouse chicks, but early indications are that these chicks were collected from a very large area. When enough harriers have been marked, future work will be concerned with defining their hunting ranges and finding what proportion of the total grouse they take.

(*N. Picozzi*)

(e) *Golden eagles* (Aquila chrysaetos), *mainly in upper Deeside*

I have studied golden eagle populations in upper Deeside since 1944. The main aim was to find the number of adult pairs every year and their breeding success. Less detailed studies were done in other parts of north east Scotland, and in some years in parts of the western Highlands. The aims in these other areas were to compare eagle numbers with fluctuations in food supply within areas, and with differences in food supply between different areas. A more recent aim on the main Deeside area has been to use the population data to see if the periods of use or lack of use of toxic pesticides are associated with any changes in eagle numbers or breeding success.

Since 1963 a golden eagle survey has been done in Scotland, with several observers studying numbers and breeding success in different regions. It was known that adult eagles and eagle eggs sent for analysis contained residues of toxic insecticides, and it was feared that these might reduce the eagles' production of young and also the adult stock. In addition, J. D. Lockie and D. A. Ratcliffe showed in 1964 that the breeding success of eagles in Wester Ross had greatly declined, and eagle eggs from this region contained residues of toxic insecticides. Eagles in western Scotland feed largely on sheep carrion, and the birds probably took in toxic chemicals used in sheep dips. Studies by the various observers for the national survey in 1964 showed that breeding was poor in most parts of the Highlands, and a decrease in eagle numbers was expected if this continued. In upper Deeside, breeding was still good, but

an eagle found dead from severe tuberculosis in this area in 1963 did have very small residues of organo-chlorine pesticides.

Nevertheless, there was no association between the intensive period of pesticide use in the early 1960's and any observed changes in eagle numbers in the Deeside region. The average brood size per successful fledging has not fallen. In 1966–68, the mean number of young reared per successful fledging was 1·4 (14 successful fledgings), compared with 1·3 from 1944–57 (51 fledgings). More birds failed to breed in 1964–65, but this fluctuated anyway from year to year in previous decades. In 1964–65, about 35 per cent. of the pairs did not breed, but approximately one in three of these involved pairs in which females were still in immature plumage. In the three years from 1966–68, only eight pairs out of 33 (24 per cent.) did not breed—not appreciably worse than the average of 20 per cent. from 1945–57. So the general picture is that the eagles are not breeding much worse. The number of adult pairs in my main study area increased by two pairs in the late 1940's during a period when the use of DDT became widespread. One of these extra pairs and one other pair disappeared in the late 1950's. This loss was in areas where the birds were not persecuted at all, and it occurred before the main period of use of the most toxic pesticides such as dieldrin, and before breeding success became poor in west Scotland. One more pair disappeared in the late 1950's. In the last few years three other pairs have been prevented from breeding successfully, all due to an increase in persecution by gamekeepers in certain areas. Only one pair disappeared in the last few years from areas without persecution, and this was in an area where one of the two extra pairs appeared in the late 1940's.

The reason why the Deeside birds do better may be that they hardly ever eat dead sheep. They feed mostly on grouse, ptarmigan, hares and dead deer in areas with little or no arable farming. By contrast, eagles in the west of Scotland feed largely on dead sheep and thus may take in insecticides from the sheep dips. It is interesting that a national survey showed continued poor breeding in the mid 1960's in the western areas, but an improvement in the late 1960's, associated with the banning of dieldrin in sheep dips. In no area did the number of adult pairs decrease greatly, though this might possibly have happened if they had bred poorly for many years.

However, even if eagles had decreased in west Scotland, there has remained a reservoir of good breeding in the Deeside—Cairngorms—Grampians region, from which other areas might be recolonised. Throughout my study from 1944 to 1970, there has been a surplus of young eagles from the Cairngorms, emigrating to areas of grouse moor in lower Deeside, Strathdon and elsewhere, that are not occupied or only sparsely occupied by adult eagles.

There is an interesting parallel with the peregrine (*Falco peregrinus*). The number of pairs and their breeding success have declined all over Britain except the east Highlands. In the Deeside region I found that the number of adult pairs (7–8) in 1963–69 was similar to what it was in years before toxic insecticides were used, and they have bred successfully; for instance six pairs that I checked in 1965 reared a total of 15 young, and a seventh pair an unknown number of young. Fledged broods have varied from one to four young each, with an average of 2·5 in 13 broods from 1965–68. As in the eagles, this may be because the adult peregrines live all year on the hill ground, and their prey is mainly moorland animals.

(*A. Watson*)

(f) *Ecology and management of Asiatic lions* (Panthera leo persica)

Asiatic lions are found at present only in the 1,265 km² Gir Wildlife Sanctuary and vicinity in Gujarat State, India. From a series of counts up to May 1968 the Gujarat State Forest Department concluded that the number of lions was declining. In April 1968 I began an investigation of the lion's status and predator-prey relationships, which lasted through to 1971. While the Forest Department census methods might not give accurate figures for lion numbers, the decline is confirmed from a significant contraction in the lions' total range since 1955.

Increases in cultivation appear to be important, particularly with the recent advent of cash money crops. In the 1950's, much of the land adjacent to the sanctuary was forested, but by 1963, 63 per cent. of all the land adjoining the sanctuary within a radius of approximately 40 km was under crops. This changed the habitat and the numbers and distribution of wild and domestic herbivores on which the lions depend. Evidence of cultivation encroachment on the sanctuary is common, particularly in the south western parts where the highest lion densities were recorded during the 1955 census. Now, there are only a few lions there. Outside the sanctuary high densities of lions were recorded only in the few forested regions not yet cleared for cultivation.

At first sight there appeared to be no shortage of available prey. Outside the sanctuary wild ungulates are so few as to be negligible, but domestic buffalo, bullocks and cows reach densities of 83 per km², based on a compilation of the district office records for each adjoining political jurisdiction. Within the sanctuary, there are approximately five wild ungulates per km² (mainly cheetal *Axis axis*), based on night road strip counting, and approximately 19 domestic bovids per km², based on a total count of a 178 km² sample area. Not surprisingly, the lions live predominately on domestic bovids within the sanctuary, and totally on them outside.

Rewards were offered to the cattle graziers for co-operating in an inquiry into their domestic losses. Out of 222 kills of bovids investigated, cows accounted for 41 per cent. Within the sanctuary, the lions were making an intense selection for cows; for approximately eight months of the year cows were only 5–9 per cent. of the resident bovids but the proportion killed was similar to outside. The loss of cows within the sanctuary is so high that the cattle graziers had to make purchases from outside to supplement their breeding stock of cows. This would otherwise have declined.

A clue to one of the lion's major constraints was revealed when the carcases were examined. Of 146 carcases the lions fed on only 114, eating nothing from 22 per cent. Similarly those carcases which had been fed upon were in general poorly utilised. There were two major reasons for this wastage. Observations of known lions showed that they were predominantly nocturnal. However, the domestic stock on which they preyed was secure within village corrals at night. 18 lion kills made within villages were investigated. In all of them the lions failed to drag the carcases beyond the village confines and lost them entirely, because the villagers drove the lions away. Not surprisingly most kills were in daylight. The domestic stock was then both away from the protective cover of the corrals and moving about in open country or in forest, where it was easier for the lions to make kills. Nonetheless the lions lost completely approximately 12 per cent. of the daylight kills.

When a lion made a daylight kill, the graziers usually drove it away by throwing stones, waving axes, shouting, and sometimes by employing a curious

rock sling device called a 'go-pan'. The lions did not return for some time, and commonly not until after dark. The graziers meanwhile returned to their village and complained of their loss, informing the Bhand harijans who claim the carcases of cattle for the hides which they sell and for the meat which they eat. Of 172 carcases investigated, the hide collectors took part or all of 51 per cent. of the kills made inside the sanctuary and 80 per cent. outside, so that they were another important influence on lions outside the sanctuary.

Most of my data on lion behaviour and population dynamics await analysis, but the preliminary conclusions are: (*a*) the numbers of adult male lions may be regulated by territorial behaviour, (*b*) the number of cubs reared by lionesses depends on food availability, (*c*) the continued survival of the lion population depends on limiting further range contraction and on maintaining the supply of domestic animals as food. Aerial surveys carried out in 1963 and in 1970 by the Defence Department, but currently not made available to the Gujarat State Forest Department, could, if declassified, be used to pinpoint rapidly many of the illegal cultivation encroachments. At least within the sanctuary it would be desirable to restrict the scavenging of lion kills by hide collectors. However, as these people depend for at least a quarter of their livelihood on lion kills, the solution would need to take this into account.

(*P. W. B. Joslin, Ph.D. Student*)

4. The Grazing Ecology of Red Deer and Blackface Sheep

Until very recently, sheep and deer have been regarded as competitors within the Scottish upland environment, and this attitude can be traced back as far as the 10th century. The reasons for this division have been largely social and economic, but it is also claimed that deer occupy land and eat grass that would otherwise be available to sheep, or vice versa. It is therefore implied that the ecology of the animals is similar and that the two species compete for scarce resources.

A review of the evidence available suggests that in general the ecology of different ungulate species often differs in such a way that the number of stock which the range can maintain without damage is higher under mixed stocking than with a single species. Furthermore, there is also evidence which indicates that mixed stocking results in better use of the vegetation. Whether such stocking results in greater financial returns depends on the relative product prices for each species. With recent increases in the price of venison, the alternatives of single or mixed stocking of deer and sheep are important questions economically; which of these alternatives is ecologically more desirable cannot be assessed until we have basic information on the extent to which the ecology of deer and sheep overlaps, and their effects on hill pastures.

In this study, I obtained information solely on grazing behaviour. The work was done near Killin, Perthshire (NN 562375) in 1967–70. The study area was about 750 ha in size, and varied in altitude from 150–910 m. The underlying rocks are primarily Ben Lawers calcareous mica-schist; the soils are base rich, with high *p*H values, and the vegetation predominantly grassy. The number of sheep on the ground at any one time varied from 200–300, and the number of deer from 50–250.

The specific aspects I studied and the methods used were as follows. Plant preferences: the proportions of plant species occurring in the faeces of sheep and deer were assessed each month by faecal analysis. Comparisons

were made between sheep and deer of (*a*) differences in the proportion of any plant ingested in any month, and (*b*) differences in the pattern of intake through the year. Sward preferences: the distribution of sheep and deer was recorded eight times per day from an observation hut. The position and activity (standing, lying) of each animal were plotted on a panoramic photomosaic and later recorded on computer punch cards in terms of the co-ordinates of a 10 m grid.

The vegetation was mapped by interpreting the photomosaic and carrying out a ground check with a two-man team equipped with radio transceiver communication. The resulting map was then transferred to a vertical aerial photograph and the vegetation boundaries recorded on punch cards using the same 10 m grid as for the animal distributions. The two sets of data (animal distribution, vegetation) were merged and analyses of animal distributions in relation to vegetation type carried out using the SPSS (1970) survey programme mounted at the Edinburgh Regional Computing Centre. Data are available for eight months of the year, and provide comparisons between sheep and deer of preference for each vegetation type in terms of the time spent on each type.

Using the data collected on activity (above), animal behaviour was analysed in terms of (*a*) changes in the proportion of animals standing or lying throughout the day and between each month, (*b*) diurnal rhythm of movement up and down the hill, and (*c*) the use of different altitudes during different months. In addition, information was obtained on nocturnal activity.

The results indicate:

(i) Qualitatively sheep and deer ate the same plant species;

(ii) Quantitatively there were differences between sheep and deer in the proportions eaten for most individual plant species during most of the year;

(iii) There were distinct differences in the pattern of intake of grasses, sedges and dwarf shrubs throughout the year; the average proportions of these groups over all months were 46 per cent., 14 per cent. and 19 per cent. for sheep, and 36 per cent, 17 per cent. and 33 per cent. for deer;

(iv) Sheep and deer used the same vegetation types but to different degrees in all months and showed differences in their distribution in relation to altitude;

(v) Diurnal patterns of grazing were quite similar, with peaks of activity around dawn and dusk, and a lull at midday but deer were much more variable than sheep;

(vi) Between dusk and dawn during summer, sheep and deer grazed for up to 17 per cent. and 66 per cent. of the time; in winter, sheep grazed up to 30 per cent. of the time and deer 78 per cent.;

(vii) Both sheep and deer had distinct and different vertical patterns of movement which varied between seasons, and in summer, between months.

This evidence suggests that the grazing ecology of sheep and deer is much less similar than commonly supposed. They frequently differ in the amount of each plant species and group eaten; they differ in their use of plant vegetation types, and show different overall preferences for altitude. Sheep show a

high degree of selectivity for certain plant species and vegetation types, whereas deer preferences, although distinct, are much less accentuated. Moreover, I could find no evidence of either species avoiding the other. Until we can identify areas likely to be overgrazed and can establish appropriate standards of plant utilisation, we cannot say with any certainty whether sheep, or deer, or both will be ecologically preferable in a given situation. Nevertheless, it is clear that in this study, where sheep and deer had the same freedom of choice, there were significant differences in the degree and timing of their choice of food. In fact the analysis suggests that the use of the vegetation by the two species together was more even than would have been expected from their behaviour if either had been there alone. However, this conclusion needs to be tested by experiment.

(I. Colquhoun, Ph.D. Student)

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