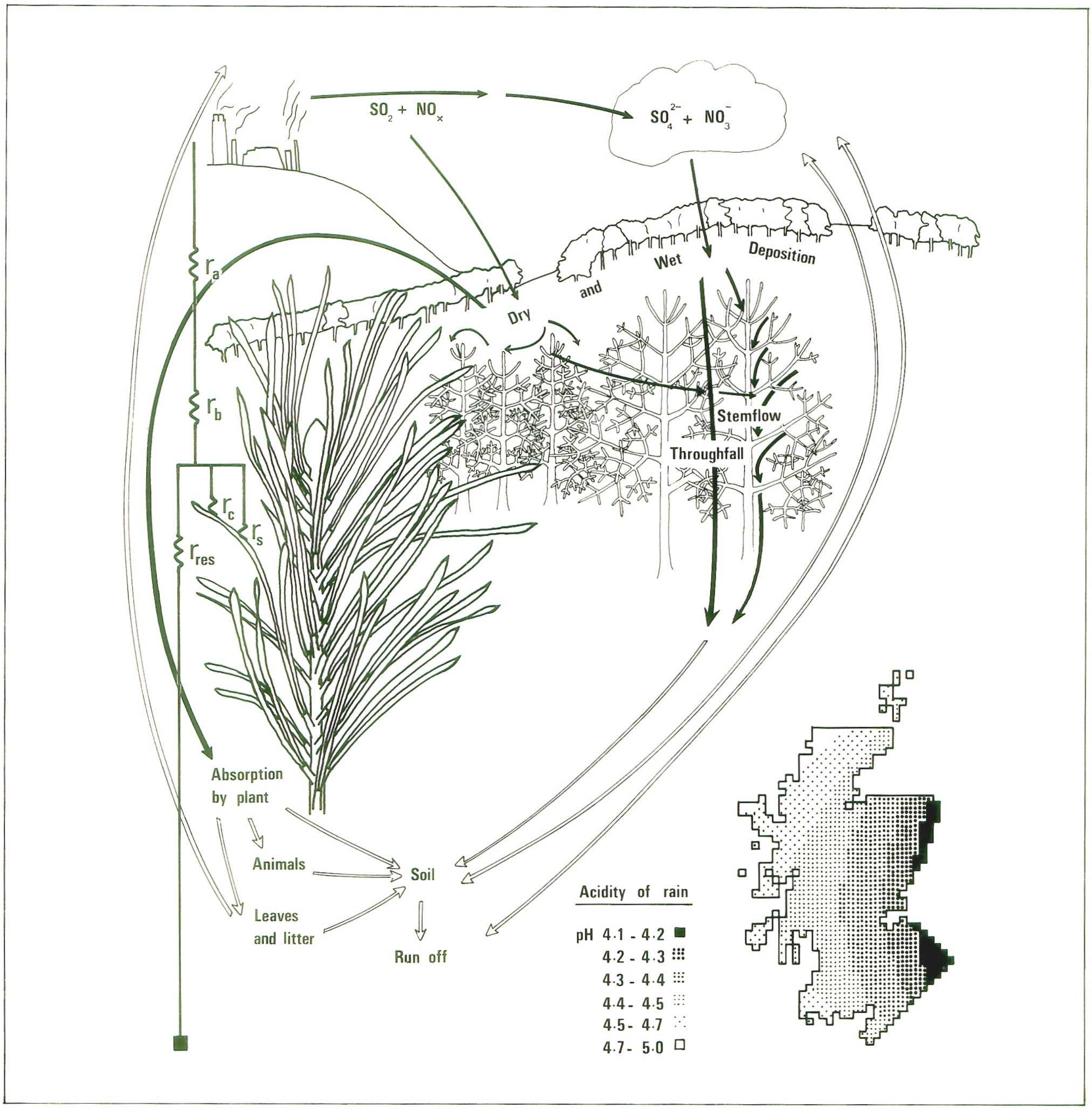
Natural Environment Research Council

Institute of Terrestrial Ecology



1981

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Annual Report 1981

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Cover design was prepared by Dr Julia Wilson of ITE Bush. It shows schematically the pathways of 'sulphur' and 'nitrogen' air pollutants in a forest. The solid arrows indicate the parts of the network being investigated within ITE.

ACKNOWLEDGEMENT

The Institute wishes to thank Miss Sarah Anthony for drawing the figures in this report. The work was carried out as part of her year's sandwich course at our Monks Wood Experimental Station, Huntingdon. Sarah is a cartography student at the Luton College of Higher Education, Bedfordshire.

The Institute of Terrestrial Ecology (ITE) was established in 1973 from the former Nature Conservancy's research stations and staff, joined later by the Institute of Tree Biology and the Culture Centre of Algae and Protozoa. ITE contributes to and draws upon the collective knowledge of the fourteen sister institutes which make up the *Natural Environment Research Council,* spanning all the environmental sciences.

The Institute studies the factors determining the structure, composition and processes of land and freshwater systems, and of individual plant and animal species. It is developing a sounder scientific basis for predicting and modelling environmental trends arising from natural or man-made change. The results of this research are available to those responsible for the protection, management and wise use of our natural resources.

One quarter of ITE's work is research commissioned by customers, such as the Nature Conservancy Council, who require information for wildlife conservation, the Department of Energy and the Department of the Environment, and the EEC. The remainder is fundamental research supported by NERC.

ITE's expertise is widely used by international organizations in overseas projects and programmes of research.

Contents

Is ecological research really necessary?

In these days of recession, when the activities of the productive and service industries are constrained by reduced demand, when local and central Government agencies are being cut back in staff and kept within strict cash limits, it is sensible to ask if the research which is done by institutes like ITE is really necessary. The question is particularly pertinent when universities are also being pruned back hard. On the face of it, scientific research into the environment might seem a luxury, and, certainly, Government Ministers and their advisers, if not Members of Parliament, seem increasingly to take this view, if we are to judge by the marked reduction in the research which is commissioned by Government departments and agencies.

The reader will hardly expect the Director of a Research Council Institute to suggest that the research his Institute does is not necessary! However, in these days of cash limits and staff reductions, it requires more than a bold assertion to justify spending money on environmental research, and the spending of that money in a Research Council Institute rather than in the universities. It is not sufficient to assert that, because the "environment" is a "Good Thing", research on the environment must, by association, also be a "Good Thing".

The major environmental problems of the 1980s in the United Kingdom were summarised briefly in ITE's Annual Report for 1980. It will, however, do no harm to repeat that summary here, not least because the warning that it contained of urgent ecological problems has largely fallen on deaf ears. The over-riding need is to ensure that the limited resources of the world are used to the best advantage, leading to an understanding that our use of these resources will place even greater pressure on the environment in the future. Much of the concern is likely to be focused on the development of energy resources, including oil, coal and nuclear power, the exploration and exploitation of which are likely to have major effects. Coupled with this search for and development of new sources of energy, pollution from new and existing industrial processes will continue to attract attention and will require critical research, especially in the fields of air and water pollution, the use of pesticides and herbicides, the identification of pathways of radionuclides, and the determination of the effects of toxic heavy metals. Politicians, resource managers and administrators continue to underestimate the importance, and urgency, of such research.

In the rural environment, the increased attention to resource utilisation is likely to place a major emphasis on land use, including the re-evaluation of policies for agriculture and forestry, and nowhere is this emphasis more likely to be felt than in Britain, where we have a high population and a relatively small land area with many competing users and agencies. In the lowlands, the policy for cheap food may lead to greater intensification of agriculture on the better soils, by increased use of monocultures over large areas, by new and greater use of pesticides, and the continued removal of marginal land (including hedges, ditches, etc). As these better soils also support the greatest diversity of wildlife, attempts to improve grassland by drainage, the use of fertilizers, or by re-seeding, with a consequent effect on herb-rich grasslands, have major effects on wildlife conservation. As a result of the intensification of agriculture and horticulture on better soils, unimproved grassland is likely to be even less actively managed than at present, and so to become scrub and woodland which will be used mainly for recreation, forestry, or energy production. The importance of external influences, including such factors as the cost of energy, climatic change, and political decisions about pricing policies in the EEC, may, in all these influences, be overwhelming. The present trend towards increased production of grass, together with the reliance on imported concentrates, also seems to indicate the need for more information about the effects of nitrogen on crop, semi-natural and natural ecosystems as a result of the marked increase in the use of nitrogen fertilizers by farmers and foresters. The presence of nitrates in water supplied for drinking represents an unacceptable hazard, and the sources of these nitrates remain largely obscure.

In the uplands, the major issue is almost certain to be the possibility of extending the area of forest, as a response to world shortages of timber and wood pulp, and the increased reluctance of exporting nations to sell the large volumes of timber which Britain imports annually. Studies of the effects of this increased area of forest, which has been variously estimated as being between 8 and 12% of the total land area, are now urgently required. Such studies will include the effects that this increased area of forest will have on the environment, and particularly on the integration of forestry with other land uses such as agriculture, recreation and visual amenity, and wildlife conservation. Such studies will not necessarily be confined to the uplands, as the relative demands for wood and food may lead to agricultural land also being used for the production of high quality and fast-growing timber. A particular problem will be the effects of forests on hydrology, water resources and water quality, especially where forests are planted in areas which traditionally supply water for major urban centres.

Even for the present relatively low proportion of land devoted to forestry, dependence on a limited range of provenances of one or 2 species by foresters during the last 30 years gives cause for concern because of the vulnerability of British forests to attack by pests and pathogens. A more effective long-term strategy for the choice of species and for methods of forest management is almost certainly necessary, especially if the area of forest is to be increased substantially. The current outbreaks of the infestations of pine beauty moth in Scotland on lodgepole pine provide an example of the dangers which have been run by an over-dependence upon a limited range of genetic material. If similar outbreaks were to occur on Sitka spruce, dependence on the widespread use of pesticides, currently regarded as the solution to the pine beauty moth infestation, might prove an unacceptable hazard to the environment. Foresters are themselves showing a renewed interest in mixtures of species as plantation crops, and there is still a great deal that is not understood about the ways in which such mixtures affect and are affected by soil processes.

There also exists a considerable area of broadleaved woodland which is currently regarded as unproductive, or even derelict, under existing forms of commercial management. Hardwood timber is likely to be an extremely scarce resource, worldwide. Such areas will almost certainly be scheduled for rehabilitation during the next decade, but care will be needed to see that minimum damage occurs to wildlife conservation, for which these woodlands provide an important resource. Stocks of selected clones of indigenous hardwoods will need to be built up if rehabilitation is to be successful.

Land use will continue to be a major issue as renewed demands are made by conservation and other bodies for a national land use policy. Such a demand assumes that an agreed policy could be negotiated, and also assumes that any negotiated policy would be more favourable to conservation than the interaction of the separate policies of land-using agencies, buffered by the general conservatism of landowners and tenants. The recent Wildlife Protection Bill, for example, has introduced a totally new situation whose effects will need to be monitored closely over the coming years. Ideally, NERC should be in a position to predict the effect of existing and proposed policies before it is too late to make the changes necessary to prevent positive damage to the environment. Even more important, however, is the need to extend the range of feasible options which are apparently being discussed by policy-making organisations. For many wildlife species, the destruction of habitat is probably the most important influence, and we will need to find ways of ensuring the compatibility of emerging patterns of land management with the maintenance of adequate habitats for wildlife. Special emphasis will probably need to be placed on rare and disappearing species, and assemblages of species, which are affected by pollutants, by exploitation for collectors, and by the disturbance of habitats or life processes, especially their regeneration. It is not often recognised that we have a totally inadequate knowledge of the population dynamics of even quite common plants and animals and are thus almost completely unable to provide for their continuing existence.

Closely associated with the protection of rare or disappearing species is the problem of the management of National Nature Reserves and other protected areas, because it cannot be assumed that merely declaring areas as reserves will necessarily ensure the survival of the species to be protected. A large part of the effort on nature conservation in Britain has been based on the concept of nature reserves in which wildlife may persist when surrounding land becomes less suitable. There is a growing worry that many reserves are not fulfilling this need, as more and more species, particularly insects such as butterflies and moths, are lost from them. Appropriate forms of habitat management are required to ensure that viable populations of these species can survive on our reserves, but the ways in which this can be achieved are largely unknown at present. In many instances, it may be necessary to recreate habitats which have been lost either from existing sources of seed and genetic material, or through systems of management which will lead to appropriate successions. The monitoring of changes in habitats designed to protect and increase levels of wildlife may thus be done through studies of population dynamics of relatively short-lived organisms, like butterflies and moths.

Closely related to these problems is the role of wildlife as reservoirs of pests and pathogens, and the epidemiology of wildlife diseases which are capable of infecting man. Examples of these kinds of problems are already attracting particular interest, as in the interaction between rabies and fox populations, and between bovine TB and badgers. Both of these existing areas of interest are centres of controversy, and the arguments will only be resolved by a clearer knowledge of the basic ecology of the organisms concerned. Precipitous action, however well-meaning, is likely to make the problems worse in the long term.

It must not be thought that the UK is the only part of the world where such problems exist. The problems of the environment are worldwide, and the book prepared by the International Union for Conservation of Nature and Natural Resources, with the advice, co-operation and financial assistance of the United Nations Environment Programme and the World Wildlife Fund (Allen 1980), puts the problem succinctly in the statement that current attempts by one quarter of the world's people to carry on consuming two-thirds of the world's resources, and by half of the people simply to stay alive are destroying the very means by which all people can survive and prosper. The World Conservation Strategy emphasises the particular problems of desertization, the destruction of tropical forest, the problems of erosion in both developed and developing countries, and the devastating effects of environmental pollution, including the use of pesticides and herbicides. Three essential components are proposed as a strategy for the successful halting of the destruction of the world's environment, namely:

i. the maintenance of essential ecological processes and life support systems;
ii. the preservation of genetic diversity;
iii. the utilization of species and ecosystems sustainably.

Accordingly, the World Conservation Strategy urges the adoption of national and international measures with 4 strategic principles:

i. integrated development of resource management;
ii. retention of the widest possible range of future options in land and water use;
iii. judicious combination of cure and prevention in the tackling of fundamental problems;
iv. focus on causes as well as symptoms.

For crop and semi-natural ecosystems alike, our present-day knowledge of nutrient cycles and pathways of pollutants is inadequate. Genetic and physiological mechanisms of even the commonest species of wildlife remain virtually unexplored. Understanding of the mechanisms and processes of succession in vegetation, including those of colonization, is limited. Even for quite common plants and animals, the importance and influence of external factors, including climate, habitat and management, on population dynamics and life cycles are only dimly perceived.

The Natural Environment Research Council (NERC) was established by Royal Charter in 1965 under the Science and Technology Act with responsibility to encourage, plan and execute research in those sciences, physical and biological, that relate to man's natural environment and its resources. Such investigations seek to provide a better understanding not only of the nature and processes of the environment in which we live and on whose resources we depend, but also of their influence on man's activities and welfare, and, of growing importance today, of man's influence on them. In the terrestrial environment, relevant to ITE's objectives, the fields of research are broadly defined by the structure, interactions and productivity of plant and animal populations and communities.

The Natural Environment Research Council carries out its research through its own Institutes and grant-aided Institutes, and by grants, fellowships, and other post-graduate awards to universities and other institutes of higher education. Some of the fundamental research that has been mentioned above can, and should, be done in universities and other institutes of higher education, and, even under present-day pressures on finance and other resources, NERC has maintained, or slightly increased, its investment in university-sponsored research. Most of the fundamental ecological research, however, is necessarily long term, requires the planned deployment of a wide range of intellectual disciplines, and involves field work on geographically widely-dispersed sites. Such research can only be done satisfactorily by NERC's own Institutes. Britain's system of Research Councils, independent of policy-advocating departments, is the envy of the world, and NERC Institutes like ITE provide exceptional value for money in both the quality and direction of their research.

Ecological research of the kinds outlined above is an essential prerequisite of informed action to reverse the current trend towards the gradual destruction of our resources in the rural environment. Particularly significant among these trends are:

i. changes in agriculture since 1945;
ii. afforestation and the possible need for even larger areas of both broadleaved and coniferous woodland;
iii. changes in freshwater systems and in estuaries as a result of land and water management;
iv. the accumulating effects of atmospheric pollutants, and radionuclides, and the steadily increasing concentrations of carbon dioxide which have indirect effects on atmospheric temperatures;
v. the effects of herbicides, pesticides and heavy metals on plant and animal organisms;
vi. the need for the conservation of habitats and species and for the management of conservation areas.

Today, under the provisions for the financing of research by commissions from Government departments, introduced in 1973 under Lord Rothschild's customer/contractor principle, a substantial part of NERC's (and hence ITE's) income has to be derived from research commissioned by "customers". Current evidence from the level and type of support for research suggests that resource managers, administrators and politicians (national and local) do not sufficiently understand the need for research, and have a naïve belief that enough is known for any sensible man to come to the right conclusions. The history of the last 100 years has shown just how wrong this view is, especially when the action taken has to be a compromise between totally different views. Frequently, management of resources is done by immediate responses to problems (Hall 1980). Associated deadlines to these responses impose quick decisions and a false air of confidence in them which can only be countered, or supported, if there has been adequate research. Britain is in danger of cutting off the supply of essential scientific knowledge, unless the support for ecological and environmental research in Research Council Institutes and in universities is maintained or increased.

J. N. R. Jeffers
Director, ITE

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Longer research reports

Introduction

This Section contains descriptions of research which has either been completed or which has reached a stage where it warrants a fuller account than the reports in Section III.

The first report presents some of the principal conclusions reached by a major study of the diversity of invertebrates on the fragmented heathlands in Dorset. Although heathland vegetation has been studied intensively, not only in Dorset but throughout Britain, the invertebrates have been neglected despite the known richness of heathlands as habitats for invertebrate fauna. Their presence and abundance were recorded from a wide range of sites, and the relevance of species-area and species-isolation hypotheses to habitat islands and problems of nature conservation were examined.

The second report describes the results of demographic studies of the establishment and succession of communities in limestone quarries. These results highlight 2 main constraints on the development of vegetation on quarry floors, namely low seedling establishment and high seedling mortality. Experimental treatments have, therefore, been proposed, and are currently being tested, to accelerate succession on bare or partly vegetated areas, the aim being to achieve a closed but species-rich vegetation and to build up a functioning ecosystem, including soil fauna, litter-feeding arthropods and phytophagous insects.

The third project described has been investigating the cause of bark stripping by grey squirrels. At least 10 areas of woodland in the south midlands have been studied to determine what squirrel populations were associated with damage. Squirrels were trapped and marked in March or early April, before the damage period in June or July, when the bark is easily removed and the sap flow is strong and rich in sugars. It is possible that the presence of many young squirrels triggers agonistic bark stripping, but it is also possible that good spring breeding is itself merely another effect of good winter food supplies resulting in a high spring population, and hence summer food shortage. If further work does not strengthen the links between damage intensity and squirrel habitat or population characteristics, then the trees themselves will have to be examined in more detail.

The fourth account is of a study to find which coastal habitats are most used by otters in Scotland, using their faeces as an index of their activity. The main study area is centred around Sullom Voe and Yell Sound, and the methods and first results for January – October 1981 are described.

The next 3 contributions are all concerned with pollutants in the environment. The first project described has been studying the movement of fluoride from plants to field voles and wood mice, and to their predators including foxes. Measurements of bone fluoride in small mammals were made at different distances from the aluminium smelter at Holyhead, Anglesey, as fluorides are produced in quantity during the smelting of aluminium, being mainly derived from the mineral cryolite which is used as a flux. Results are given for 3 series of observations in 1977, 1979 and 1981.

The second contribution is a fuller account of the work to determine the cause of the mass bird deaths in the Mersey estuary, outlined in last year's Annual Report. Assuming that waders and ducks respond to lead poisoning in much the same way as starlings, experiments confirmed that bird deaths on the Mersey were primarily the result of contamination of the environment with alkyl lead compounds. The results also suggest that birds containing more than 0·5 mg Pb kg^{-1} as alkyl lead have changed internal and physiological features which will reduce their survival prospects. Many thousands of birds using the Mersey estuary – one of the most important overwintering grounds for ducks and waders – may be at some risk from the sublethal levels of alkyl lead compounds they contain.

The third contribution describes a contract with the Department of Environment to review monitoring within Great Britain of the biological effects of pollutants. Although pollutants act on individual organisms, it is the impact on populations that is important, apart from man and his cultivated and domesticated species. Deaths of individuals do not necessarily affect the population because high death rates may be offset by improved survival of the remainder.

The next report reviews recent work in northern Britain on the ecology of fungi forming sheathing mycorrhizas with native birch and introduced Sitka spruce and lodgepole pine, monitoring seasonal changes (epidemiology) and effects on host survival and growth. During the past 5 years, the production of mycorrhizal fruit-bodies, usually in the autumn, has been shown to be over-ridingly influenced by host factors, and experiments are investigating the abilities of early- and late-stage fungi to establish mycorrhizas in field crops when subject to competition from soil microbes.

The ninth and final contribution in this Section is an account of a recent symposium held in Grange-over-Sands to honour Charles Darwin on the centenary of the publication of his famous book 'The formation of vegetable mould through the action of worms', and to review the current state of knowledge on earthworms.

Over 140 scientists from 30 countries attended the conference, and contributions showed that Darwin's concepts are still the cornerstones of soil ecology today. Some of the papers which are particularly relevant to terrestrial ecology in Britain are discussed.

THE DIVERSITY OF INVERTEBRATES ON FRAGMENTED HEATHLAND IN DORSET

(This work was largely supported by Nature Conservancy Council funds)

Extensive reduction in area and fragmentation have affected almost all the semi-natural communities of Britain in recent years. One of the best documented examples is the heathlands in the Poole Basin in south-east Dorset (Moore 1962; Webb & Haskins 1980). In 1978, a detailed survey was made of the remaining fragments of these heathlands, recording the extent of the principal vegetation associations and storing the data for computer analysis (Webb & Haskins 1980; Webb 1980). Although heathland vegetation has been studied intensively, not only in Dorset but throughout Britain, the invertebrates have received scant attention (Gimingham *et al.* 1979), despite the considerable reputation of heathlands in southern England among entomologists.

The heathlands of the Poole Basin lie within a small well-defined area of tertiary deposits, with a uniform climate and soil. There is a wide range of heathland fragments remaining at varying distances from one another, which provide an interesting 'natural' experimental design for examining the patterns of distribution of heathland invertebrates. During 1979, the fauna of these heathlands was studied, first to record the presence and abundance of species from a wide range of sites, and, second, to examine the relevance of species-area and species-isolation hypotheses to habitat islands and problems of nature conservation.

Twenty-five sites on mature dry heathland were chosen from those surveyed in 1978, representing the entire range of sizes from 500 ha to 0·1 ha, at varying distances from each other (Figure 1). The invertebrates were sampled by pitfall trapping and vacuum sweep netting, the same sampling effort being made on each site irrespective of its size. Scores for the presence of plant species showed that the smallest sites had the greatest number of species within the area of the traps, and that sites with heathland nearby had fewer species than those which were isolated (Table 1).

Table 1. Correlation between species richness (S) of plants and heathland area and degree of isolation

	Site area (ha)	Heathlands within a radius of 1 km	Heathlands within a radius of 2 km
Plants	−0·532 ($P<0·02$)	−0·630 ($P<0·01$)	−0·543 ($P<0·02$)

Mature dry heathland vegetation is characterised by its low plant diversity and is dominated by *Calluna vulgaris*, growing in association with 4 or 5 other species, such as *Erica cinerea, Ulex minor, Ulex gallii, Agrostis setacea, Molinia caerulea* and *Pteridium aquilinum.* The additional species found on the small isolated sites were colonists from surrounding areas.

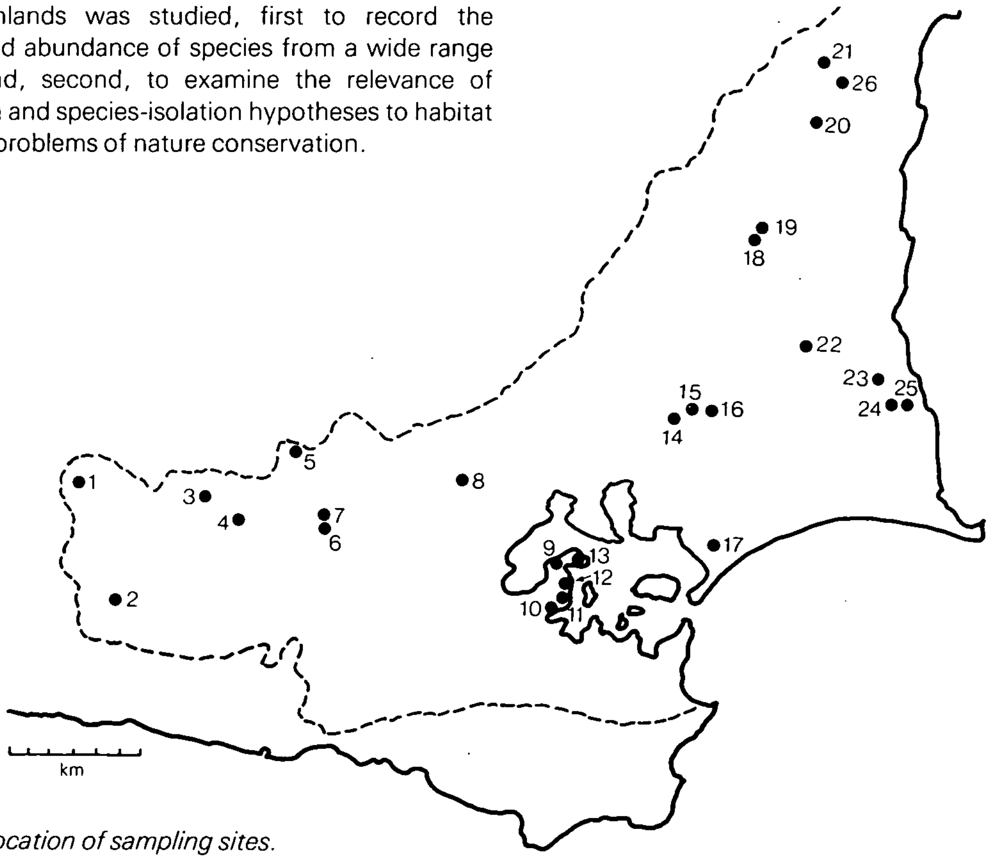
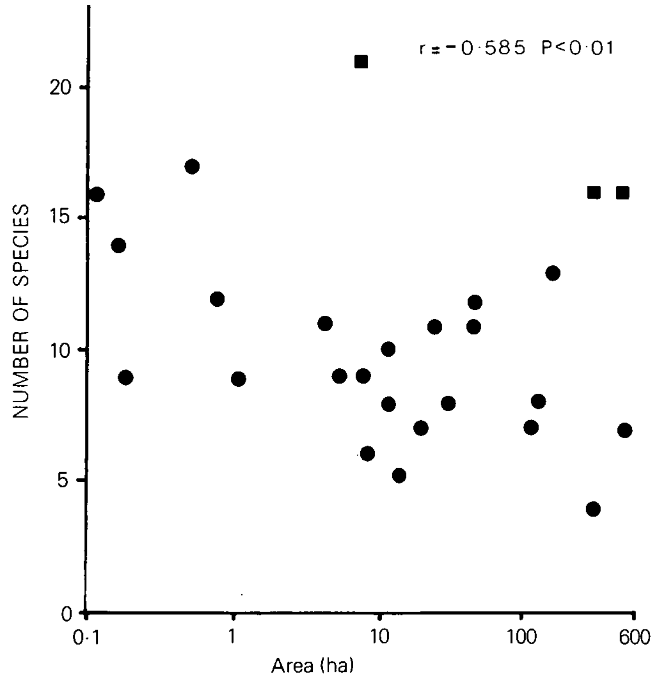


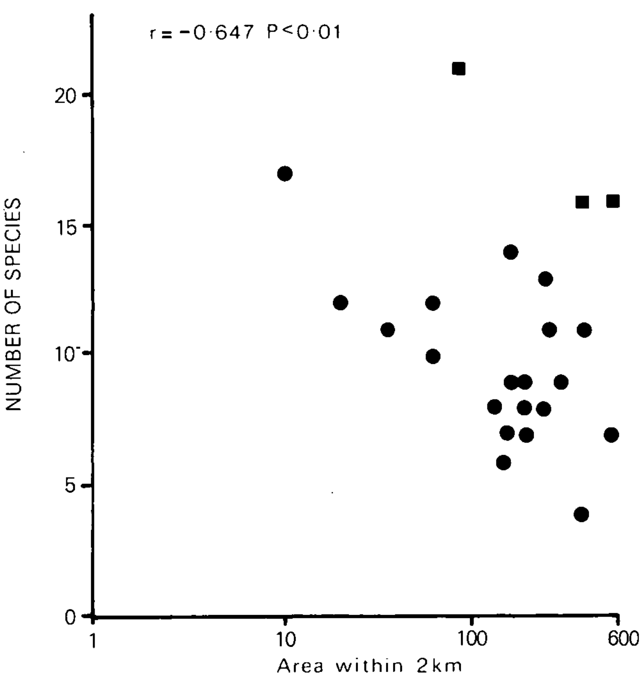
Figure 1 Location of sampling sites.

Similar trends were found for many of the invertebrates. For Coleoptera (272 species), phytophagous Coleoptera (67 species), Heteroptera (29 species), and 57 species of combined minor groups, the richness of species at a point was found to be negatively correlated with the area of heathland sites and with the area of heathland within one and 2 km radius of the sampling sites. Figures 2 and 3 summarise the results for phytophagous beetles, and the values of the correlations are given in Table 2.



67 Spp PHYTOPHAGOUS BEETLES

Figure 2 The relationship between the number of species of phytophagous beetles and the area of the site.



67 Spp PHYTOPHAGOUS BEETLES

Figure 3 The relationship between the number of species of phytophagous beetles and the extent of isolation of the site.

Table 2. Correlation between species richness (S) of plants and heathland area and degree of isolation

	Site area (ha)	Heathlands within a radius of 1 km	Heathlands within a radius of 2 km
Beetles	−0·414	−0·594	−0·583
Phytophagous beetles	−0·585	−0·483	−0·697
Heathland Heteroptera	−0·271	−0·386	−0·463
Spiders	−0·065	−0·324	−0·256
Heathland spiders	0·378	0·243	0·242
Other groups	−0·429	−0·377	−0·443

Significance levels: $P<0{\cdot}10$, $r = 0{\cdot}360$; $P<0{\cdot}05$, $r = 0{\cdot}413$; $P<0{\cdot}01$, $r = 0{\cdot}526$

The order Coleoptera (beetles) is a taxonomic, rather than ecological, grouping of species. Information on the habits and ecology of species is insufficient to recognise a group of heathland species. Sixty-seven phytophagous species from the families Carabidae, Chrysomelidae, Attelabidae, Apionidae, Cuculionidae, and Scolytidae were selected for separate analysis. These phytophagous species showed a stronger negative correlation between species richness and site area and its degree of isolation than all beetles combined. Heathland Heteroptera, another ecological grouping of species, showed the same trend. With most groups of phytophagous invertebrates, species richness would be expected to be correlated with the richness of plants, or, perhaps, with vegetation structure, rather than with other features of the habitat. Multiple regression analysis showed that 71% of the variation was contributed by 5 variables. The richness of the species of phytophagous beetles was negatively correlated with the percentage cover of *Calluna*, the percentage of grass species, and the percentage of bare ground. Positive values were obtained between species richness and the percentage cover of dwarf gorse (*Ulex minor*), and with the variability of the percentage of vegetation cover. These analyses suggest that there is an increasing number of species where there is the greatest floristic heterogeneity in the habitat, not simply a greater diversity of plant species, but also differences in the vegetation structure.

The richness of spiders (158 species) at each site was not significantly correlated with either site area or its degree of isolation. Heathland species (60), when analysed separately, showed a weak positive correlation with site area (larger heathlands have a richer fauna of spiders than small heathlands), but no significant correlation was found between species richness and degree of isolation of the sites. The richness of species of spider, as carnivores, can, perhaps, be expected to be correlated less with the composition of the vegetation and more with its structure, or the presence of suitable prey. Multiple regression analysis for all species of spider showed that there were 3 variables which contributed 43% of the variation in species richness, ie total cover of plants (negative), percentage of bare ground (negative), and variability in total plant cover (positive). These results suggested that spiders required a habitat of a particular structure for the greatest richness of species. Simple correlations between species richness of invertebrates and of plant species gave poor results. Sites with a high floristic diversity did not necessarily have the highest diversity of invertebrates, although both invertebrates and plants showed negative correlations between site area and its degree of isolation. These results, in conjunction with the multiple regression analysis, suggest that habitat structure is an important factor in determining the richness of the invertebrate fauna.

The greater species richness of the small isolated heathlands is thought to be caused by the presence of species from the surrounding areas (edge species), and partly by the effects of succession. Heathland is an artificially maintained climax, and, once factors arresting succession, such as grazing and fire, are removed, the succession proceeds through scrub to woodland. The rate of succession may depend on the degree of isolation of the site and the composition of the vegetation surrounding the area. Surroundings strongly influence small isolated sites, and there is a tendency for more edge species on isolated sites than on those which are larger or less isolated, many of which will be transient or vagrants. Large sites can be considered as having a zone around their periphery, with a fauna transitional between that of heathland and of the surrounding vegetation. The extent of this peripheral zone is unknown, and was not measured in this survey. Small sites may lie entirely within such a zone, and their fauna will be entirely composed of transitional species.

Ordinations of the heathland vegetation on the sample sites showed that sites could be separated, first, into those where *Ulex gallii* grew, and, second, according to the amount or abundance of *Calluna vulgaris*. Cluster analysis of the sites, based on their vegetation composition, confirmed this trend. *Ulex gallii* sites tended to form a cluster, as did most of the larger sites, together with some of the medium-sized sites. Small sites did not form a cluster themselves, but were distributed throughout the other clusters; they were not alike among themselves. The geographical position in the Poole Basin of the sampling sites was not reflected in the composition of the vegetation.

Ordinations of the species composition of phytophagous beetles, heathland Heteroptera and heathland spiders were carried out, but the results were difficult to interpret. The variation in composition of these species groups was not easily reduced to a few components, suggesting that the composition of the invertebrate fauna of these sites may be multivariate. Cluster analysis of the sites, based on the composition of the invertebrate fauna, revealed no meaningful clusters, and no difference in composition could be found which could be attributed to the geographical locations of the sites in the Poole Basin. There was no simple relationship between the area of a heathland site and the presence and abundance of the invertebrate species occurring on it.

It was considered that the traditional concept of species-area relationships and theories of island biogeography were not helpful in analysing the presence and abundance of invertebrate species on these heathlands. It was also suggested that heathland nature reserves needed to be as large as possible to conserve the invertebrate fauna typical of mature dry heath, because of the effects caused by species from the surrounding habitats. The lack of any consistent pattern of variation in the composition of the invertebrate fauna of the sites suggested that, for nature conservation, reserves may be selected equally throughout the Poole Basin.

Full details of this invertebrate survey are given in Webb (1981).

N. R. Webb

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ESTABLISHMENT AND SUCCESSION OF COMMUNITIES IN LIMESTONE QUARRIES

Natural recolonization and succession in chalk and limestone quarries have led to the development of attractive and species-rich communities in many parts of the country (Davis 1979). However, the rate of successional change in quarries is usually slow so that, unless deliberately restored in some way, they often remain rather barren for long periods of time. Few even medium-term studies have been made of primary succession in such derelict sites, but an understanding of the factors involved may be of use in attempts to restore natural communities.

Three main processes may be distinguished:

1. influx and retention of seeds and propagules from adjacent areas;
2. natural establishment, survival, growth and reproduction of plants in quarries;
3. disturbance factors, such as rabbit grazing.

A 3-year study of seedling demography on limestone and chalk quarry floors has been made, and experiments on accelerating natural succession have been started.

The demographic studies were divided into (i) an examination of natural seedling communities in a disused limestone quarry, and (ii) experiments on seedling establishment on bare limestone and chalk in 2 currently worked quarries. A disused area of Clipsham quarry, Leicestershire, was chosen for studies of a sparse quarry floor community, and the flora has been described by Davis' (1981). Aspects of seedling demography were studied, first by direct observation of permanently marked areas of quarry floor when emergence, survival, development and composition of seedling populations were monitored (Plate 4); second, by observation of individual species, noting development, survival and seed production; third, by artificially sowing small areas of floor with common species and monitoring the behaviour of the resultant seedling populations. Several general conclusions were made from these separate studies.

1. The seedling community consisted of about 40 species, of which 80% was made up of 17 species.
2. Establishment from known seed populations was low; generally, under 30% of the available seed emerged (Figure 4).
3. Emergence varied greatly from place to place on the floor, between seasons and years, and between species.
4. Seedling survival varied between species of similar and dissimilar life history, from place to place on the quarry floor, and between cohorts emerging at different dates.
5. Seedling development in perennial herbs was slow (Figure 4), none growing to more than 3–5 cm within 3 years.
6. Seedling mortality, particularly amongst perennial species, was high: most species suffered 60–70% mortality during the first year, with only 2–10% surviving to the second year.

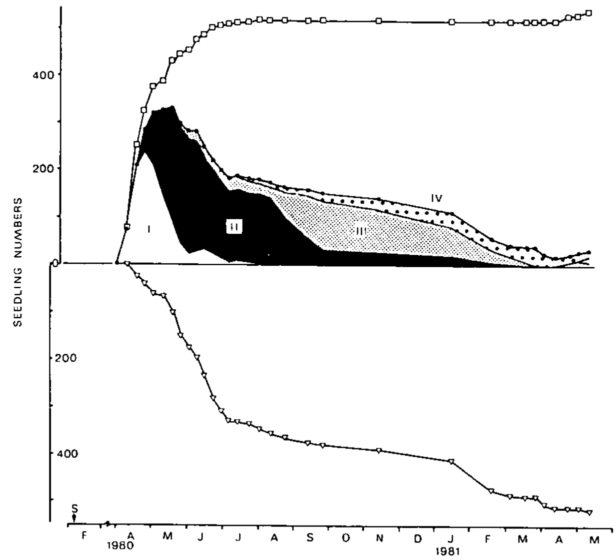

Figure 4 Seedling population flux for a sown plot of Origanum vulgare *on a limestone quarry floor.* □—□ *cumulative gains;* ∇ — ∇ *cumulative losses;* ●—● *net population present.*

I = seedling with cotyledons
II = seedling with one/first pair of leaves
III = seedling with two/second pair of leaves
IV = immature plant

7. Periods of high mortality occurred at different times during the different years. The actual causes of death could not be determined for most seedlings; however, mortality increased during periods of dry weather or after heavy frosts. The effects of rabbit grazing were also noted (Figure 5).

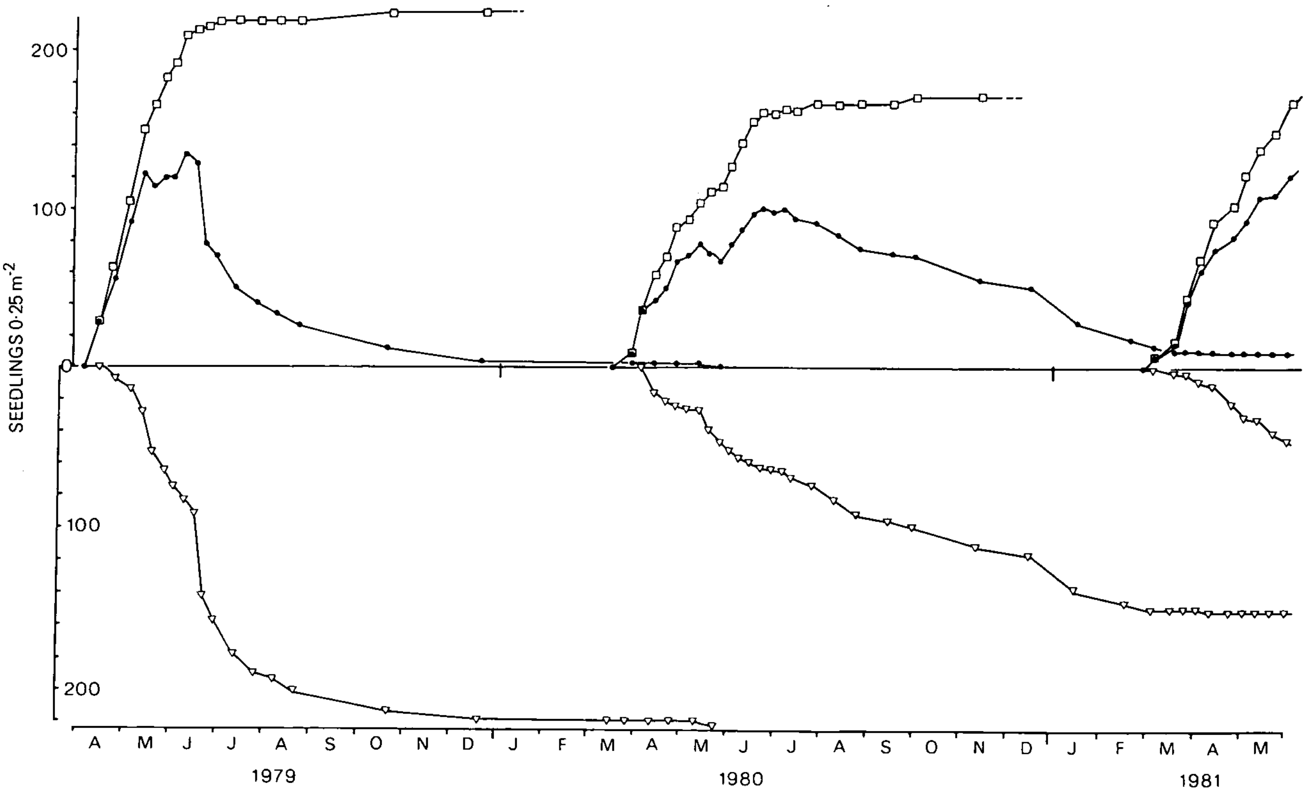

Figure 5 Population flux of natural seedling communities in marked plots (0·25 m²) (symbols as in Figure 4).

8. Annual species produced seed, but no perennial species germinating in 1979 or 1980 produced flowers by 1981 in any of the areas under observation. Seed production in established perennials was greatly below that reported for the same species in other habitats.

These findings highlight 2 main constraints on the development of vegetation on quarry floors — low seedling establishment (passage from seed to emerged seedling) and high seedling mortality. These constraints were investigated experimentally at Ketton quarry, Leicestershire (limestone) and at Barrington quarry, Cambridgeshire (chalk), using the species selected from those commonly found growing in disused calcareous quarries. The experiments demonstrated several important features.

1. The limestone and chalk quarry floor materials were poor in the major plant nutrients (Table 3), and frequently experienced acute water deficiencies under field conditions.
2. Low seedling establishment was mainly the result of actual seed loss through burial, or removal by wind.
3. Application of low levels of inorganic fertilizer generally improved seedling survival, increased seedling biomass, and increased the number of individuals producing flowers.
4. Application of water by direct irrigation generally improved seedling survival, but species with very small seedlings suffered increased mortality through erosion.
5. Small rates of application of a sawdust mulch greatly increased seedling emergence and survival. The main effect of the mulch was to increase soil moisture by 2—4% (Figure 6).

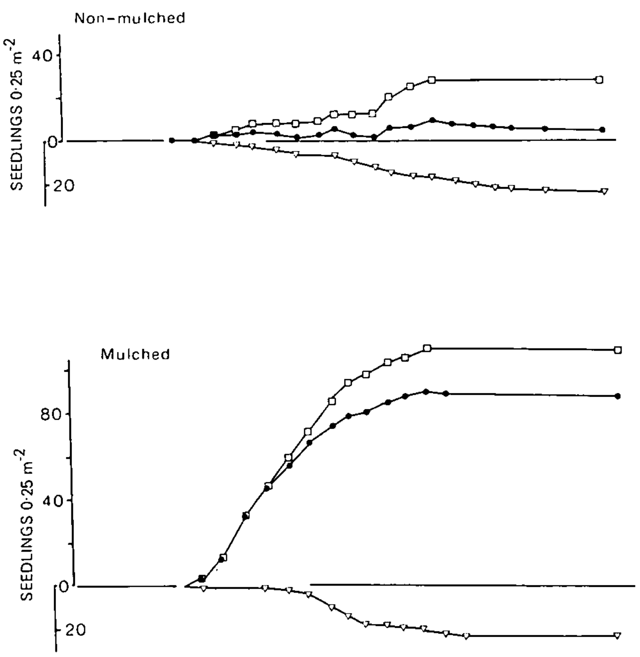

Figure 6 The effect of sawdust mulch on seedling establishment and survival in Origanum vulgare *(symbols as in Figure 4).*

Table 3. Levels of plant nutrients in the top 5—6 cm of quarry floor at Clipsham, compared with the levels in an old pasture nearby (Means ± standard deviations)

	Total % N	Extractable ppm P	Extractable ppm K	Extractable ppm Mg
Clipsham quarry	0·08±0·02	3·2±1·1	55·4± 9·6	79·1± 7·0
Old pasture	0·79±0·06	23·5±2·6	268·0±124·0	213·0±26·0

Two experiments have been started which aim to accelerate succession on a bare area and on a partly vegetated area at Clipsham quarry. The objective is to achieve a closed, but species-rich, vegetation, and to build up a functioning ecosystem including soil fauna, litter-feeding invertebrates and phytophagous insects. Three treatments have been applied in replicated combinations to 1 m^2 plots: the use of a native grass *(Brachypodium sylvaticum)* and native legume *(Lotus corniculatus)* to act as 'nurse crops' for other species; the addition of small quantities of inorganic fertilizers; and cages to protect plants from rabbit grazing for all, or part, of the year. All 3 treatments have had noticeable effects in the first season, which are expected to be cumulative.

All invertebrate populations are at low density. Litter-feeding arthropods consist principally of 2 species of woodlice, the oribatid mite fauna is likewise dominated by a few, mainly surface-living, species, whilst the phytophagous insect fauna is represented mainly by a few species of herb-associated chrysomelid beetles and leaf-hoppers (Auchenorhyncha). A modest earthworm population with 5 species has become established. Changes in all these groups will be monitored.

D. G. Park and B. N. K. Davis

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BARK STRIPPING BY GREY SQUIRRELS

Grey squirrels *(Sciurus carolinensis)* cause considerable damage in Britain by peeling the bark from stems and branches of young hardwood trees, especially sycamore, beech and oak. After removing and dropping the hard outer bark, the squirrels scrape off and eat the sap-containing vascular tissues underneath. Damaged trees may then die, or remain deformed. Stripping usually occurs in June or July, when the bark is easily removed, and the sap flow is strong and rich in sugars. However, damage does not occur in all areas of vulnerable young trees, and does not occur every year in any one area.

Of 9 hypotheses advanced in the literature to explain bark stripping, only 4 were consistent with the data available at the start of this study: that the damage results from squirrel hunger, a liking for sweet sap, trace nutrient deficiency, or some form of agonistic display (review in Kenward 1981). Food shortage was suggested by the ease of trapping squirrels in mid-summer, at a time when main spring foods have declined, but autumn seed crops are not yet available. A predilection for sweetness has been found in laboratory rats, which will take a saccharine solution of no food value in preference to a less sweet sugar solution; the trees most consistently stripped by squirrels are sycamores and other maples, trees well-known for the high sugar content of their sap. That agonistic behaviour might cause stripping was suggested by observations of squirrels gnawing during aggressive conspecific encounters in enclosures. The first 3 years of this project have been spent examining the food shortage, sap sweetness, and agonistic behaviour hypotheses. The possibility of a trace nutrient deficiency has not been investigated in detail, partly because this hypothesis seemed least likely to cause the local and annual variation typical of bark stripping, and partly because the extensive analyses necessary would have been extremely costly.

The first year was spent developing techniques and obtaining background information on squirrel populations in 3 damage-prone woods on the Elton estate, on the Cambridgeshire – Northamptonshire border. Radio tagging has been used to investigate squirrel foraging behaviour during and outside the damage period (Plate 5). This work has shown that main food and feeding areas change markedly just prior to the damage period (Kenward 1980).

After initial modification, the radio collars proved to have no adverse effects on squirrel recapture rates, weight changes and range sizes, compared with retrapped untagged squirrels (Kenward 1982). Transmitters have now been put on squirrels 162 times, and used to provide data on mortality and dispersal for combination with trapping results in a 3-year study of squirrel population dynamics in the Elton woods, which are isolated by 2·5 km from other woodland suitable for squirrels.

At first, it was intended that removal experiments should be used to investigate causes of damage. Removing squirrels from damage-prone parts of the woods in spring would reduce food depletion for the remainder, but might encourage immigration and hence agonistic encounters. Decreased damage, coupled with high squirrel weights and little immigration in an experimental wood relative to a control, would support the food shortage hypothesis, inasmuch as high weights indicate an abundance of food. On the other hand, increased immigration and enhanced damage in the experimental wood could support the agonistic behaviour hypothesis, unless squirrel weights there were reduced, in which case the immigration might simply have caused food shortage. After spring removal of squirrels from the experimental wood, there was a greater squirrel weight increase than in the control wood, and little immigration. The weight increase was consistent with the idea of an alleviated food shortage. However, there was little damage in either wood in that year, possibly because of increased food availability in new neighbouring wheat fields at the control wood, which were extensively exploited by the squirrels.

The outcome of this experiment was inconclusive, but gave some support to the food shortage hypothesis. The main conclusion was that more background information was required on the likelihood of damage, before further experimental testing of hypotheses. At least 10 areas of woodland in the south midlands have therefore been studied to determine what squirrel population characteristics were associated with damage. Squirrels were trapped and marked in March and early April, before the damage period, but at a time when squirrels are easy to catch, and retrapped in late June and July after bark stripping had started. Between these periods, the areas were surveyed regularly for damage. Legg multiple-capture live-traps were set at a density of 2 per hectare, in the same site in each trapping period, using the same pre-bait and setting regime throughout. Information was collected on squirrel densities, weights, immigration and production of spring young, in relation to the intensity of bark stripping. In the 10 areas covered during 1980, a total of 591 squirrels were trapped, 31 – 124 per area.

Figure 7 shows the weights during the damage period of trapped yearling squirrels (often called sub-adults, but in fact capable of breeding) in late summer. Adult weights followed the same trend, but differed from yearling weights in ways consistent with the adult

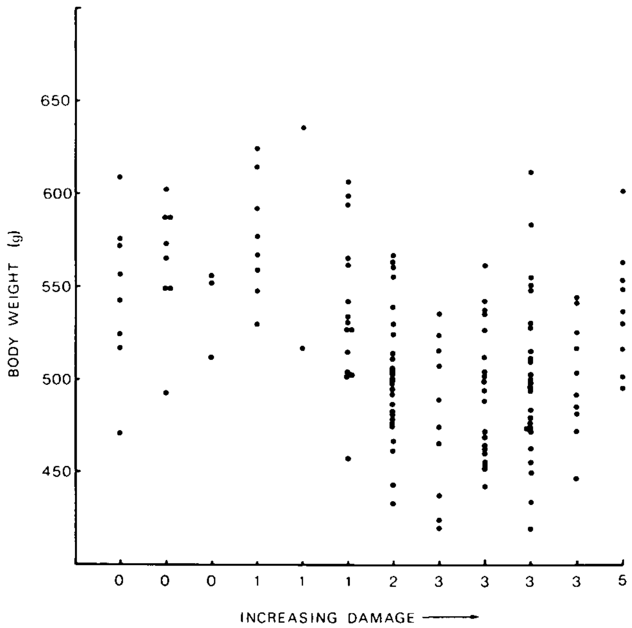

Figure 7 Weights of yearling squirrels, corrected to standard body size, caught during the bark stripping period in woods with differing intensities of damage. Damage categories are: 0 = no sign of damage; 1 = 'trials', of no more than 5 cm², on a few trees; 2 = patches of up to 250 cm² on a few trees; 3 = larger patches stripped from a few trees; 4 = large patches stripped from many trees; 5 = extensive bark stripping on most trees.

breeding activity. The weights were all corrected for body size variation using tibia length, a parameter which proved easy to measure in the field, was repeatable in live and dead squirrels, and explained 23% of body weight variation. Comparing woods, there was a significant trend of decreasing average weight with increasing intensity of damage, except that the weights in the most heavily damaged wood tended to be higher than in other damaged woods. Moreover, the weight change per day between the first and second trapping periods was inversely related to damage intensity: squirrels lost most weight in the most damaged areas. However, because the study had been permitted in some areas on condition that the squirrels were trapped and killed when damage started, there had been a tendency to trap the damaged areas first. Since there were too few traps to cover more than 3–4 areas at once, and trapping sessions took 14 days, 3 sessions over 6 weeks were needed to trap all the squirrels. Thus, although at least one undamaged area with relatively heavy squirrels was covered at the same time as the most damaged areas with the less heavy squirrels, a general seasonal tendency for squirrel weights to increase during June and July could have accounted for some of the observed association between low weight and damage. The results, therefore, demonstrated that squirrels stripped bark at a time of year when their weights were low, but did not show clearly that low weight at the same season was associated with bark stripping.

There was no evidence that bark stripping was associated with spring immigration into a population, but there was a tendency for the most damaged areas to have had the highest production of spring young. High production of spring young could have increased food shortage through population increase, or increased agonistic encounters, or both.

Other weight data support the food shortage hypothesis. The weights of squirrels in the Elton woods in July show a highly significant negative trend, with increasing intensity of bark stripping between 1978 and 1981. Moreover, the heaviest, annually most persistent damage occurred in areas where overwinter feeding of pheasants, or livestock, was producing high squirrel densities in spring, which might therefore be out of balance with limited food supplies in summer. The importance of this additional food was evident at Elton, where all radio tagged squirrels regularly visited pheasant food sites, and where early cessation of pheasant feeding in 1980 was immediately followed by increased dispersal and mortality of squirrels.

As the 1980 data suggested associations between food shortage and damage, but not conclusively, the exercise was repeated in 1981, using new areas in some cases and obtaining more traps so that the summer trapping could be completed within one month. Trapping was also conducted without the tendency for the most damaged areas to be covered first, and an assessment was made of winter food by estimating abundance of conifer cones, acorns and other mast crops.

The results confirmed the association between damage and low squirrel weights, although the relationship was not as marked as in 1980. Once again, there was a tendency for the heaviest, most regular damage to occur where squirrel weights were higher. However, squirrel weights were also much the highest in spring in the most damaged wood, so that their weight loss in mid-summer was greatest. It is also possible that, once squirrels have learnt to strip bark, they will do so again next year, even if food is not as scarce. The 1981 results confirmed the tendency for production of spring young to be high in damaged areas, and showed that this productivity, together with spring density, was linked to winter food abundance. The results are therefore somewhat ambiguous. It is possible, for instance, that the presence of many young squirrels triggers agonistic bark stripping, but it is also possible that good spring breeding is itself merely another effect of good winter food supplies resulting in a high spring population, and hence summer food shortage.

It is important to resolve these alternatives, and this will be the main aim of field work in 1982. Intensive radio monitoring in 3 areas will seek to relate food shortage and bark stripping in individual squirrels, and to investigate whether agonistic encounters (which can be heard from some distance away) and bark stripping are greatest in areas used by newly-emerged spring young. Subsequent experimental addition, or removal, of squirrels will then be planned to test the most likely hypothesis. If mid-summer food shortage is the main cause of extensive bark stripping, then future research will seek summer foods which might be made more abundant in vulnerable woodland. On the other hand, if agonistic encounters caused by young squirrels are a major cause of bark stripping, then the urgency of work at Reading University to develop contraceptive foods for squirrels will be enhanced. In either case, it seems likely that reducing the squirrel winter food supply will help to prevent damage, by reducing the population size. Modern lowland woods, in which rows of beech or oak main crop alternate with rows of a conifer early crop, provide excellent winter food for squirrels, with a variety of possible seed crops, and the conifers tending to bear cones at an earlier age, and more often, than in denser stands. It may be possible for woodland management to reduce these foods, including the use of tree strains which seed later in life. Increased prediction of damage likelihood, by observation of seed crops in vulnerable areas, could also reduce the number of expensive trapping programmes needed. It is already clear that squirrels should be trapped in woods where feeding of game, or livestock, artificially enhances winter food supplies. Operating traps at these feeding stations involves little extra work, the cost of which is probably covered by the reduction in the amount of food taken by the squirrels, let alone the reduction in subsequent bark damage.

It remains possible that neither high squirrel density relative to food nor agonistic encounters are the real cause of bark stripping, but that both are related to weather, or other variables, that influence the attractiveness of trees for stripping. This hypothesis could explain why squirrels in enclosures still strip bark despite *ad lib* feeding and before the emergence of young, although such stripping could also be an artefact of other conditions of captivity. Tree attractiveness was initially investigated in terms of sap sugar concentration. Unexpectedly, chemical analyses showed a slight inverse relationship between sugar concentration and the extent of bark stripping on different beech and sycamore trees (Figure 8a). It now appears that the most damaged trees were those with the greatest volume of sap per unit area (Figure 8b), and hence the most sugar (and protein) per unit area stripped, despite the slight decrease in sugar concentration with increasing sap volume. Obtaining sap at 0·5 litre m^{-2}, a squirrel needs to strip about 0·5 m^2 per day to obtain its daily energy requirements from sap sugar and protein alone, a rather large amount of bark stripping by normal standards. However, the volume needed may be reduced by caecal digestion of cellulose ingested as phloem structural tissue; also, bark is not the only food eaten at such times.

There is considerable variation in both sap volume and sugar concentration among stripped trees, and perhaps local and annual variation in sap volume or sugar content can account for some variation in the occurrence of damage. It is also possible that variation in the presence of an as-yet-undetected chemical is involved, eg an aversive substance or trace element. If further work does not strengthen the links between damage intensity and squirrel habitat or population characteristics, then the trees themselves will have to be examined in more detail.

R. E. Kenward

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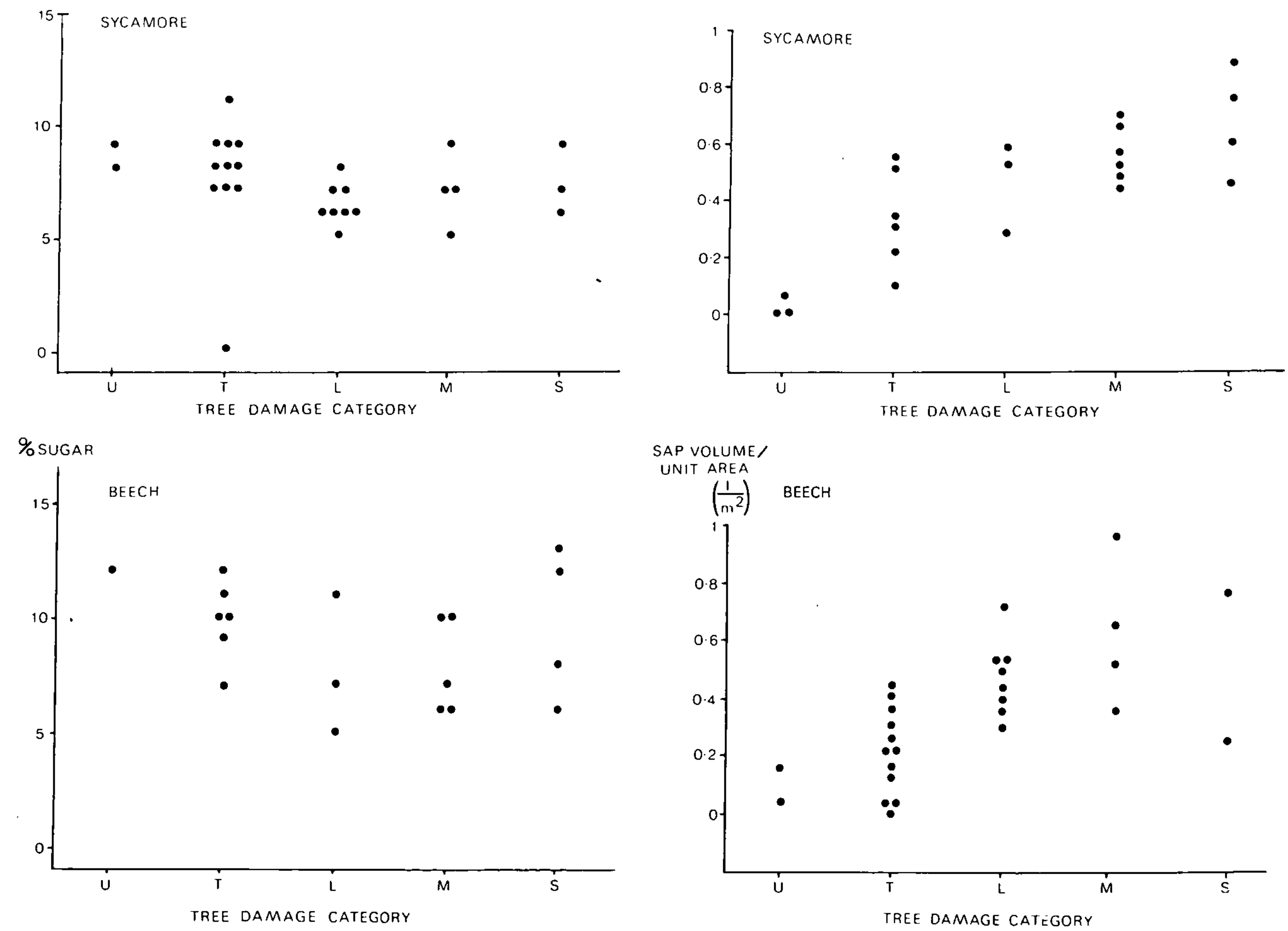

Figure 8 The sap sugar concentration (a) and sap volume (b) from trees in various damage categories: U = no bark stripping; T = <5 cm^2; L = 5–250 cm^2 stripped; M = 250–10 000 cm^2 stripped; S = > 10 000 cm^2 stripped.

METHODOLOGY FOR STUDYING HABITATS USED BY COASTAL OTTERS

(This work was largely supported by funds from the Shetland Oil Terminal Environmental Advisory Group (SOTEAG))

The aim of this study is to find which coastal habitats are most used by otters in Shetland, using their faeces (spraints) as an index of their activity. This report describes the methods and first results for January—October 1981, especially the selection of sample lengths of coasts, the proportion of spraints found, and tests of the validity of underlying assumptions and of the methods used. Jenkins and Burrows (1980) used spraint density as an index of otter behaviour in freshwater habitats in Aberdeenshire, but did not discuss the validity of the methods used.

The main study area is centred around Sullom Voe and Yell Sound, the region with which SOTEAG is chiefly concerned (Figure 9). It includes:

1. The area in Yell Sound from the Point of Fethaland (National Grid reference HU 379951) to the eastern end of Lunna Ness at Stour Hevda (HU 524732) on the mainland, the Island of Yell from North Taing (HU 535797) to Ramna Geo (HU 472966), and its smaller islands. The coastline includes all the shores contaminated by oil in a major spill from the Esso Bernicia in 1979 and the coasts near the tanker route to and from the oil terminal at Calbeck Ness.

2. A 'control' selection of other nearby coasts (Figure 9), in case the usage of the coasts around Sullom Voe by otters is already atypical because of the development and previous pollution.

Tankers approach Shetland from any direction. When they are unable to enter the terminal because the port is closed, they wait in Colgrave Sound. An oiling incident could, therefore, occur on almost any Shetland coast, and all the types of coast in the islands are included in the areas of study.

The main problems being studied are:

1. Do the frequency and distribution of otter signs vary on different types of coast, and can different coastal habitats be ranked in the frequency with which these signs occur?

2. Do the frequencies of occurrence of otter signs vary with the time of year?

Survey areas

Over 2 years, 1981 and 1982, the islands are being visited for 3 weeks in each calendar month, with 12 trips altogether. Previous studies of coastal otters in Scotland found about 1 km between occupied holts, and the aim was to sample coasts over distances potentially large enough to include at least one centre of otter activity. Assuming that otter activities centre on holts, 2 km was selected as the standard length of coast for sampling, and, whenever possible, each section is examined on foot from the high tide mark to about 15 m above the head of the beach (in 3 surveys each over 1 km in different habitat types, over 95% of the spraints found were within 15 m of the head of the beach).

Lochs within 100 m of the shore are examined and streams are followed for at least 50 m from their mouths, details of width, depth and speed of flow of the streams being recorded, along with the presence of pools.

As far as possible, each section of coast is of uniform habitat type, but the coasts of Shetland vary over short distances from sandy beaches to 100 m high cliffs. In this initial analysis, the major habitat type of the section is taken as representative of that length of the coast.

Milner (1975) categorised major coastal habitats in Shetland. From a sample of over 1700 points, each chosen at the intersection of the 1 km grid on the coast on the Ordnance Survey maps (scale 1:63 360), he identified 8 major coastal types, using 81 physical and 18 geological attributes. Pollution, human habitation and disturbance were not included, but are being recorded in the present survey, together with other features such as details of coast exposure, species and density of seaweed, nature and contour of the seabed immediately offshore, the width of the intertidal zone, the nature and biological composition of the terrain immediately behind the coast, and nearby lochs and streams, which may affect the distribution of otters. In all, our classification has over 200 attributes, which are grouped under 7 heads (Table 4) for this initial analysis, but will need to be refined and enlarged in later analyses. The total coastline in the study area measures about 250 km. Division into approximately 2 km sections resulted in 107 workable sections and 11 islands.

Table 4. The main habitat types, their frequency of occurrence and number to be sampled in the study area

Habitat type	Number of sections	Number to be sampled
I Cliff-backed (>5 m) sheltered* coast	8	2
II Cliff-backed (>5 m) exposed coast	22	5
III Boulder/bedrock coast, sheltered and with a medium steep gradient	9	2
IV Boulder/bedrock coast, sheltered and with a gentle gradient	14	2
V Boulder/bedrock and exposed coast	12	2
VI Sand shingle coast, sheltered and with a medium steep gradient	8	2
VII Other shingle coasts	31	7
Additional samples		
Islands	13 (11 islands)‡	
Calbeck Ness**	3	3

*Exposed coast is taken as coast with more than 2 km of open sea between it and the nearest coast opposite

**Sullom Voe terminal

‡Each island will be visited 3 times altogether

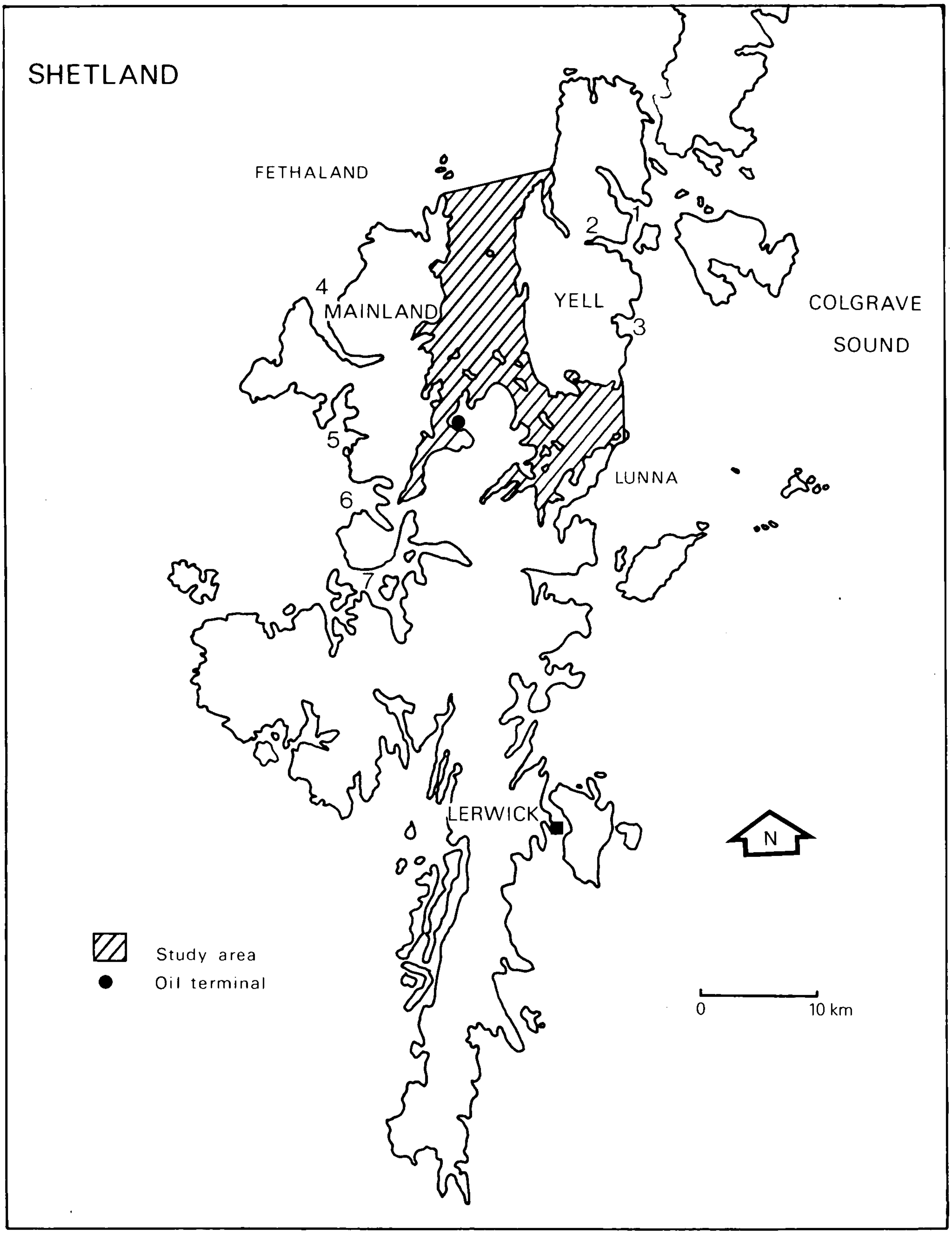

Figure 9 The study area and the selected study voes: 1 Basta Voe; 2 Mid Yell Voe; 3 Otterswick; 4 Ronas Voe; 5 Gunnister Voe; 6 Mangaster Voe; 7 Voes and firths of Swarbacks Minn.

Because of the distances involved, it is not possible to survey the whole coast on each trip. A preliminary visit to the islands in October 1980 showed that 22 sections could be surveyed in a 3-week period, and it was decided that the same 22 sections would be examined on each visit (intensive study area). These 22 sections were selected at random, but in proportion to the major habitat types in the area, and included at least 2 examples of each habitat (Table 4). The whole of Calbeck Ness, the site of the oil terminal (3 sections), is also surveyed on each trip; the remaining 82 sections and the 11 islands comprising the total length of coast in the Sound will be visited at least 3 times during the study.

Table 5. The percentage of artificial spraint sites set out by one person and found subsequently on a single walk by a second observer

Habitat type* / quality	Numbers of sites set out by first person	Numbers of sites found by second observer	% found by observer
II – poorest	47	41	87·2
III – intermediate	48	39	81·3
V – best	40	34	85·2
Total	135	114	84·4

*Assessed from observed densities of otter spraints

A comparison with Milner's survey shows that the shores of our study area contain representatives of all the types of coast found in Shetland. Coasts under cliffs cannot be surveyed adequately from the shore, but can be viewed from a boat and checked by occasional landings. For these difficult areas, indices of numbers of otters seen are calibrated against frequencies of observations at other sites, where numbers of spraints are counted more easily. These observations will be reported later.

Signs of otters

1. Spraint sites and spraints Sites are defined as places with several spraints, or spraint piles, occurring within 1 m. Long-established sites on grass tend to be bright green, and are usually on prominent features such as knolls and boulders. Sites are marked by numbered plastic pegs and photographed. Spraints more than 1 m from each other or divided by a definite barrier, eg a river mouth, are recorded separately. Where possible, the actual number of individual spraints is counted, but, where large piles of spraints are found, an estimate of the number is given. Dry and fragmented spraints are discounted, but anal jelly is recorded.

2. Otter tracks On soft sand, mud and snow, otter footprints are easily identifiable and are measured to indicate the presence of young animals.

3. Sightings Observations of otters form an important part of the survey, particularly under cliffs. Whenever otters are seen, numbers, approximate size (small, medium or large) and behaviour are recorded, and movements along coasts are followed to assess range. Time, sea conditions and state of tide are noted.

4. Other observations Resting, lie up, rolling and drinking/washing places are also recorded.

Before the observations can be assessed, it is necessary to know the limitations of the techniques used. As otters may spraint at sea, in burrows or in other inaccessible places, it is impossible to find all the spraints dropped in a section. The main questions are:

1. Is the initial assumption valid that spraints can equally easily be found on all types of coast?

2. How often should each sample area be searched on each visit? Do the numbers of spraints and sites found increase, if the number of searches increases? If no increase is recorded despite 2 further searches, the number found is defined as the 'findable' spraints.

3. What is the minimum number of visits necessary to each habitat to find an acceptable proportion of 'findable' spraints?

Ideally, all 'findable' spraints should be recorded, and it is necessary to assume that the proportion of these is similar in all habitats. In practice, the time and effort required to find 100% may be disproportionate to the value of finding an arbitrarily smaller proportion, say about 80%.

Findable spraints

Comparing habitats The aim was to discover whether similar proportions of spraint sites were found in different coastal habitats. One person laid out an undisclosed number of 'spraint sites' (marker pegs) in each of 3 habitat types – V 'best'; III 'intermediate'; II 'poorest' – in places where otters would spraint naturally. A second person (the observer) then walked each section, picking up all the 'sites' found. Table 5 shows that the observer found 81–87% (mean 84·4%) of the total number of artificial sites in all 3 habitats. The initial assumption is, therefore, taken to be correct, ie similar proportions of spraints and spraint sites will be found in different habitats.

Repeated searches The aim was to determine how many times a section needs to be walked to record all the 'findable' spraints. Tests were done in 9 2 km sections, representing all 7 coastal habitat types, each section of near uniform habitat throughout, and it was assumed that every 'findable' spraint site had an equal chance of being found within each habitat type. Each section was walked 6 times on consecutive visits, and all the spraint sites were mapped (scale 1:50000) and numbers of spraints at each site counted. The total cumulative numbers of spraints (541) and sites (138) detected on all walks together were assumed to be the number of 'findable' spraints. (A danger in this method is that the observer remembers where he saw spraints on a previous visit, but this should not affect the conclusions, as the main aim was to find the cumulative total.)

On average, 78% of the findable sites were found on the first search, increasing cumulatively to 91% and 97% on the second and third searches, and 100% on the fourth search (Table 6). In all habitat types, all the findable sites were recorded by the fourth search. The 34 sites missed during the first searches were much smaller in size, having fewer spraints (mean 1·8) than the remaining 104 sites (mean 4·6, $t=10{\cdot}2$, $P<0{\cdot}05$), but were in similar places. On average, 85% of the spraints found were recorded on the first search.

Table 6. The percentages of spraints and spraint sites found on each of 6 successive searches along 9 sections of coast representing all 7 main coastal habitat types in the study area

Habitat type	Total found	Cumulative proportion found Visit 1	2	3	4–6
Spraint sites					
I	4	75	100	100	100
I	5	60	80	100	100
II	8	75	88	100	100
III	24	77	87	96	100
IV	37	81	87	97	100
IV	32	75	90	100	100
V	11	81	100	100	100
VI	14	79	86	92	100
VII	3	67	100	100	100
Mean		78	91	97	100
Spraints					
I	15	93	100	100	100
I	23	78	91	100	100
II	32	81	91	100	100
III	62	82	92	98	100
IV	128	89	97	99	100
IV	116	89	95	99	100
V	31	87	100	100	100
VI	118	87	98	98	100
VII	16	81	100	100	100
Mean		85	96	99	100

Comparing observers The aim was to determine what proportion of spraints found by one observer was found by a second person. The first observer marked all the spraints he could find in a section during several visits (this cumulative total was taken as the absolute number of spraints). The second observer repeated the search, mapping the spraints he found on a single visit (giving a number for the 'findable' spraints for the second person). In 4 tests, in 3 different habitats, the proportion found by the second observer varied between 76–90% (mean 81%) of the total recorded by the first observer (Table 7), which is similar to those in previous tests.

Table 7. The percentage of marked spraints found by one observer on several visits and recorded subsequently by a second observer on a single visit

	Spraints marked by first observer (n)	Spraints found by second observer (n)	(%)
	37	29	79
	21	19	90
	46	40	86
	48	37	76
Total/mean	154	125	81

Observer efficiency

The same observer An observer's ability to find spraints/sites could improve with increased experience (he could record a higher proportion of findable spraints on a second or subsequent search), with increased knowledge of the habitat, or at different seasons (changes in habitat cover could affect the likelihood of finding spraints). To monitor such possible changes, one section of each habitat was surveyed twice on each trip to the islands. Table 8 shows that new sites not recorded on the first walk were recorded on the second walk in all habitats on the first 2 trips (January – February and March – April), whereas no new sites were found on the second walk in one habitat in May – June and July, in 3 habitats in August, and in 4 habitats in September – October, suggesting that observer efficiency gradually improved from 0–40% on second walks. However, because over 80% of the spraints were always found on the first visit, right from the start, this apparent increase in efficiency is unlikely to affect the conclusions.

Different observers The aim was to compare the number of spraint sites and spraints recorded by different observers on the same section of coast on a single visit. Two 4 km stretches were surveyed by 4 different observers, who worked in pairs, starting at opposite ends, and mapped every spraint found (Table 9). The total numbers of different sites mapped by the 2 pairs of observers together were 33 and 28 in the 2 tests. These are the findable sites, between 78–82% of which were found by each observer. However, only 60–64% of the findable spraints were found by both observers. In this case, the stretch of coast examined was twice as long as usual, and over 50% of the sites missed were in sections surveyed after 2·5–3 hours. In the first 2 hours of this test, 82–86% were found by all 4 observers, and, of the 21 sites found by only one observer, 14 contained 3 or fewer spraints.

Conclusions

1. A single search on each coastal type visited gives an adequate index of the number of findable spraints or sites.
2. Different observers of similar experience are expected on average to work with similar efficiency.
3. The maximum duration of a survey should be 2 hours, after which efficiency wanes and a break is necessary.

D. Jenkins and J. W. H. Conroy

Table 8. The number of spraint sites found on each of 2 successive searches at each habitat type during 1981

Habitat type	January – February a	b	c	March – April a	b	c	May – June a	b	c	July a	b	c	August a	b	c	September – October a	b	c
I				9	10	10	12	12	0	13	16	9	3	5	40	6	8	25
II				4	5	20	6	7	14	4	4	0	3	3	0	4	4	0
III	9	11	18	11	14	21	21	23	9	16	18	11	12	15	20	17	17	0
IV	40	49	18	18	19	5	16	19	16	21	24	13	18	22	18	21	24	13
V	29	33	12	62	67	8	53	58	9	47	51	8	42	45	7	67	72	7
VI				21	26	19	22	25	12	9	12	25	7	7	0	9	9	0
VII				12	15	20	9	11	13	4	5	20	5	5	0	7	7	0
Percentage zeros recorded on second walk			0			0			14			14			43			57

a – Number of spraint sites recorded on first survey
b – Number of spraint sites recorded on second survey
c – % of new sites found on second survey

Table 9. Comparison of 2 pairs of observers working independently along the same section of coast on a 3–5 h walk

Test	Observer pair	Cumulative total number of sites found by both observers	Number of sites found by each observer	Number common to both observers	% total sites found	% common to both observers
1	A B	33	27 27	21	82 82	60
2	A C	28	24 22	18	80 78	64

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FLUORIDE IN SMALL ANIMALS

The importance of fluoride in the environment has been recognised for many years, especially since Roholm (1937) showed that large amounts can be damaging to humans. In addition to occurring naturally, fluorides often arise as unwanted by-products of industrial processes, particularly when materials from the earth's crust are heated, as in the manufacture of steel, glass, cement, pottery and bricks. Fluorides are also produced in quantity during the smelting of aluminium, being mainly derived from the mineral cryolite ($Na_3Al\ F_6$) which is used as a flux.

In the USA, amounts of fluoride in animals and plants have been examined in areas of Montana contaminated by fluoride by-products from phosphate fertilizer production and aluminium smelting. In particular, the smelter at Columbia Falls, because it is close to the Glacier National Park, has been the subject of several investigations (Carlson 1973; Gordon 1974; Kay *et al.* 1975a, b). In Britain, Wright *et al.* (1978) assessed the amounts of fluoride in small mammals from the vicinity of a recolonized fluorspar tailings dam in Derbyshire. Elsewhere, amounts of fluoride in uncontaminated ecosystems have been investigated (Kay *et al.* 1975a). In New Zealand, Stewart *et al.* (1974) determined the amounts of fluoride in wildlife prior to the opening of a large aluminium smelter at Invercargill.

In 1970, an aluminium smelter, with an annual capacity of 100000 tonnes, started production at Holyhead on Anglesey, an island in north Wales which, until then, was largely concerned with agriculture and tourism. Some aspects of contamination from this smelter have already been investigated and described (Perkins *et al.* 1980a, b). This contribution is concerned with the movement of fluoride from plants to herbivores (field voles and wood mice) and to their predators including foxes. Measurements of bone fluoride in small mammals were made at different distances from the Holyhead smelter.

The simplified pathway in Figure 10 assumes that:

i. fluoride in soil originates from bedrock and/or aerial contamination and can be taken up by, or deposited on, plants;
ii. small mammals, such as field voles *(Microtus agrestis)* and wood mice *(Apodemus sylvaticus)*, acquire fluoride by eating plants. The main foods of voles are various species of grass (Ferns 1976);

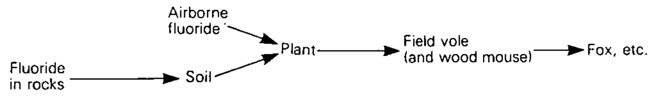

Figure 10 Pathways of fluoride.

iii. foxes *(Vulpes vulpes)* and other predators acquire fluoride by eating small mammals: field voles form 50% of the diet of lowland foxes (Lever 1959; Englund 1965; Kolb & Hewson 1979).

Material and methods

Small mammals were caught alive in Longworth traps and killed with chloroform before being sexed and weighed. Skin and viscera were removed and bodies put into a 10% solution of papain which digested soft tissues from the bones in about 12 h at 65°C. Because most of the fluoride in vertebrates is found in their skeletons, attention was focused on the analysis of bones, although some measurements were made on other tissues. A set of the main long bones was retained from each animal, while fluoride concentrations were measured in either the bulked remainder of the skeleton or the skull and jaws, the cleaned bones having been dried for several days and then ground to pass through a 600 micron sieve. Fat was not removed from the bones.

Fluoride concentrations were measured following the method described in Allen *et al.* (1974); a direct-reading Orion Ionalyzer meter was used in conjunction with a specific ion electrode. Cross checks were made of the results obtained in ITE and laboratories elsewhere in Britain.

Amounts of fluoride were measured as $\mu g\ g^{-1}$ but are quoted as the more familiar parts per million (ppm).

Results

Three series of observations were made, in 1977, 1979 and 1981.

1977: Samples were collected at 8 locations, each with a radius of 1 km (Figure 11). The smelter was in the centre of site A, whereas sites C–H were 5, 10 and 15 km along north-east and south-east transects. Site B was about 4 km to the west. At least 5 animals of each species were collected every 3 months at each site (published fluoride analyses suggested that these numbers would enable 100% differences to be detected).

The concentration of fluoride in wood mice was greatest near the smelter and least in animals caught at distances of 15 km (Figure 12). In field voles, differences in mean concentrations of fluoride were smaller (Figure 13) and, although the highest concentration was again nearest the smelter, there was a minor peak 5 km distant along

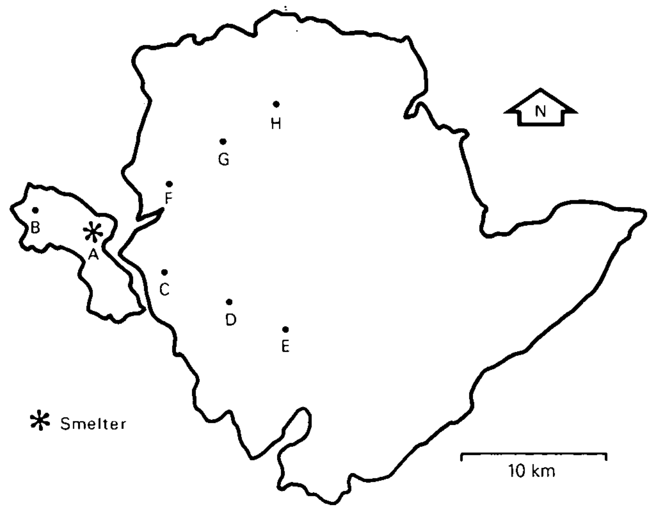

Figure 11 Map of the island of Anglesey showing 8 sites where small mammals were trapped in 1977.

the NE transect. Inspection of the data for both field voles and wood mice indicated that there were at least 2 groups of each species near the smelter. Field voles had mean fluoride concentrations of either 350 or 2450 ppm and wood mice had mean concentrations of either 1350 or 7000 ppm.

Fluoride concentrations in voles varied most from May–June onwards, possibly because of the appearance of young animals with relatively small concentrations of fluoride, the amounts of fluoride being age-related (Walton 1981). Unfortunately, it was difficult to sort young from old animals by their physical features, although they could often be identified by their amounts of fluoride.

1979: Observations were restricted to field voles trapped monthly from February 1979–January 1980 in a small plantation mostly of lodgepole pine *(Pinus contorta)* planted in 1970 about 1 km south of the smelter already mentioned. Concentrations of bone fluoride were of the same order as those detected in the more contaminated population (A_1, see Figure 13) at site A in 1977. Mean concentrations reached a peak in June becoming minimal in August when most of the animals appeared to be juveniles (Figure 14). Juvenility was judged by body weight and by the weights of eye lenses which were dissected from freshly killed animals and transferred to formalin before being weighed dry. In the event, body weights and weights of eye lenses were positively correlated. Additionally, fluoride concentrations in bone (skull and jaws) were positively correlated with body weights and weights of eye lenses (Table 10).

1981: A few wood mice and field voles were trapped in the second half of 1981 at a site 200–300 m downwind from the Anglesey smelter. The bone fluoride concentrations were usually even larger than those

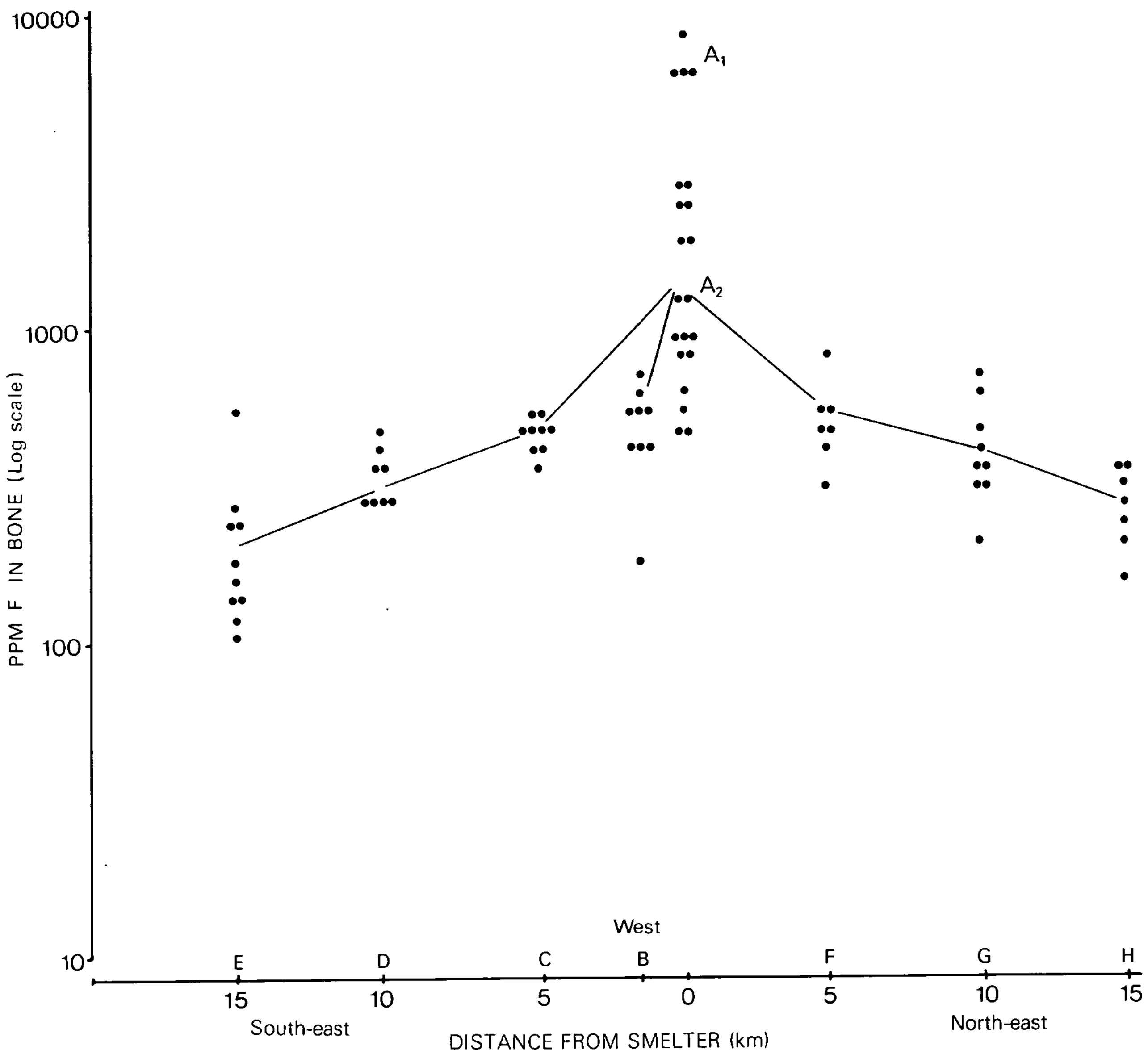

*Figure 12 Concentrations (ppm) of fluoride found in bones of wood mice (*Apodemus sylvaticus*) at the different sampling locations in February – March 1977 (see Figure 11). Near the smelter at site A, there seemed, judging by fluoride concentrations, to be 2 populations of wood mice A_1 and A_2 (lines are drawn between mean values).*

Table 10. Correlation coefficients indicating relationships between (i) body weights, (ii) weights of dried eye lenses, and (iii) bone (skull and jaw) fluoride concentrations in field voles *(Microtus agrestis)* trapped February 1979–January 1980 in a forest plantation 1 km south of the Holyhead aluminium smelter (df = 103; P<·001)

	Body weight	Weight of dried eye lenses	Bone fluoride concentration
Body weight	1·00	–	–
Weight of dried eye lenses	0·48	1·00	–
Bone fluoride concentration	0·50	0·53	1·00

detected in 1979, with an upward trend from 2800–4900 ppm in August to 10 000 ppm in December, and with some individuals having as much as 2% fluoride (Table 11).

Discussion and interpretation

Several problems arise when attempting to assess accumulation of fluoride. First, which tissue or tissues should be examined? Most research workers have chosen bones, because a large proportion of ingested fluoride can be found in them, but this is not to suppose that lesser concentrations may not have profound effects on soft tissue. Although, in the present study, the concentrations of fluoride in liver and kidney were relatively small, differences were related to differences in amounts in bone (Table 12).

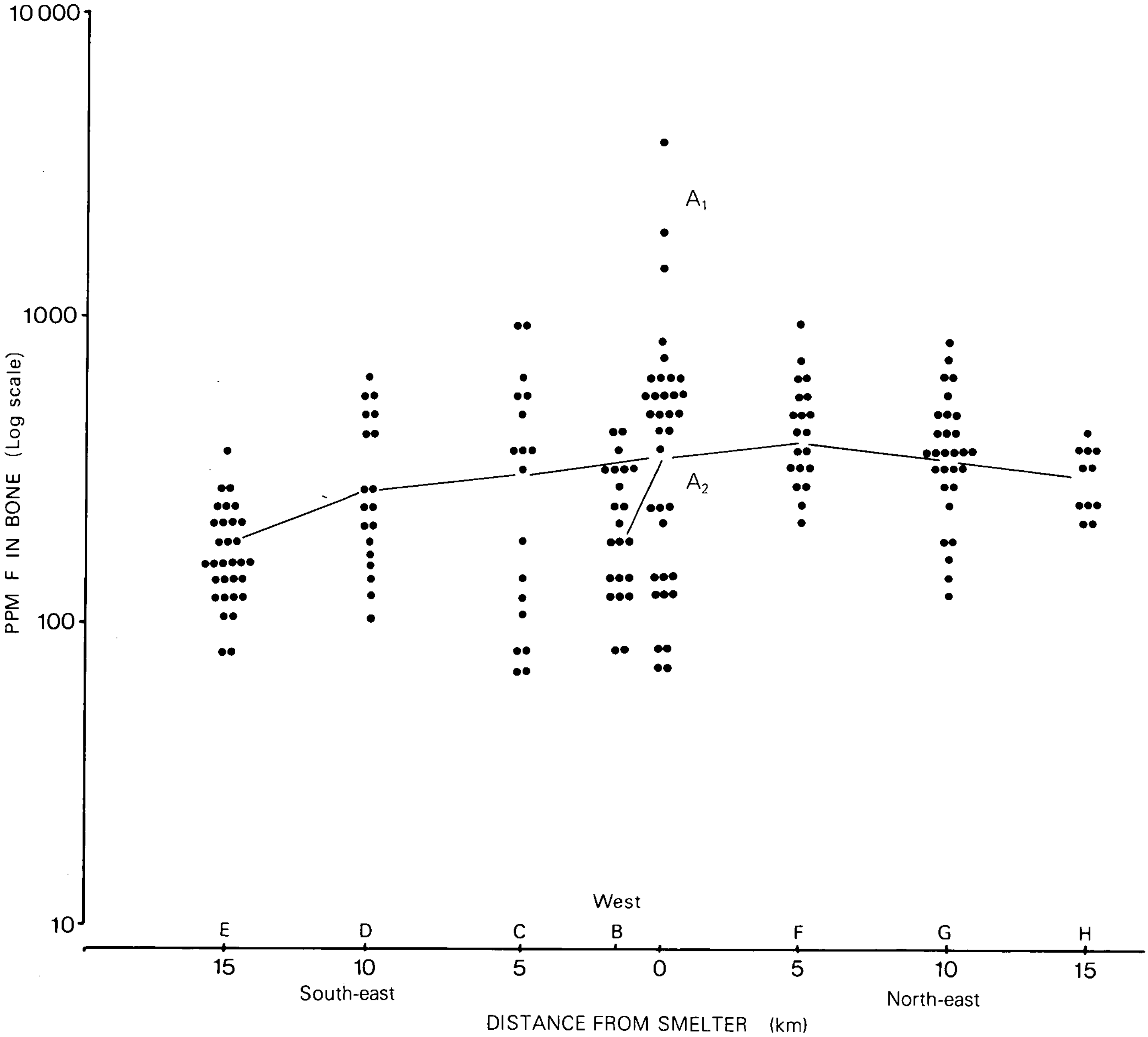

*Figure 13 Concentrations (ppm) of fluoride found in bones of field voles (*Microtus agrestis*) at the different sampling locations in February — December 1977 (see Figure 11). Near the smelter at site A, there seemed, judging by fluoride concentrations, to be 2 populations of field voles A_1 and A_2 (lines are drawn between mean values).*

Table 11. Mean concentrations (ppm) of fluoride in bones of wood mice and field voles trapped 200—300 m east of the Holyhead smelter in the second half of 1981

	Animals trapped in					
	August		September		December	
	Numbers caught	Mean concentration	Numbers caught	Mean concentration	Numbers caught	Mean concentration
Wood mice	3	2800	7	8000	9	10200
Field voles	1	4900	8	8000	1	9900

Table 12. Mean concentrations (ppm) of fluoride in the bones, liver and kidney of wood mice and field voles near the Holyhead smelter.

	Type of tissue					
	Bone		Kidney		Liver	
	Numbers examined	Mean concentration	Numbers examined	Mean concentration	Numbers examined	Mean concentration
Field voles*						
a	8	7600	8	130	8	43
b	19	1600	10	103	17	27
Wood mice	7	510	4	57	7	19

*Field vole populations sampled: a 200—300 m, b 2 km from the smelter

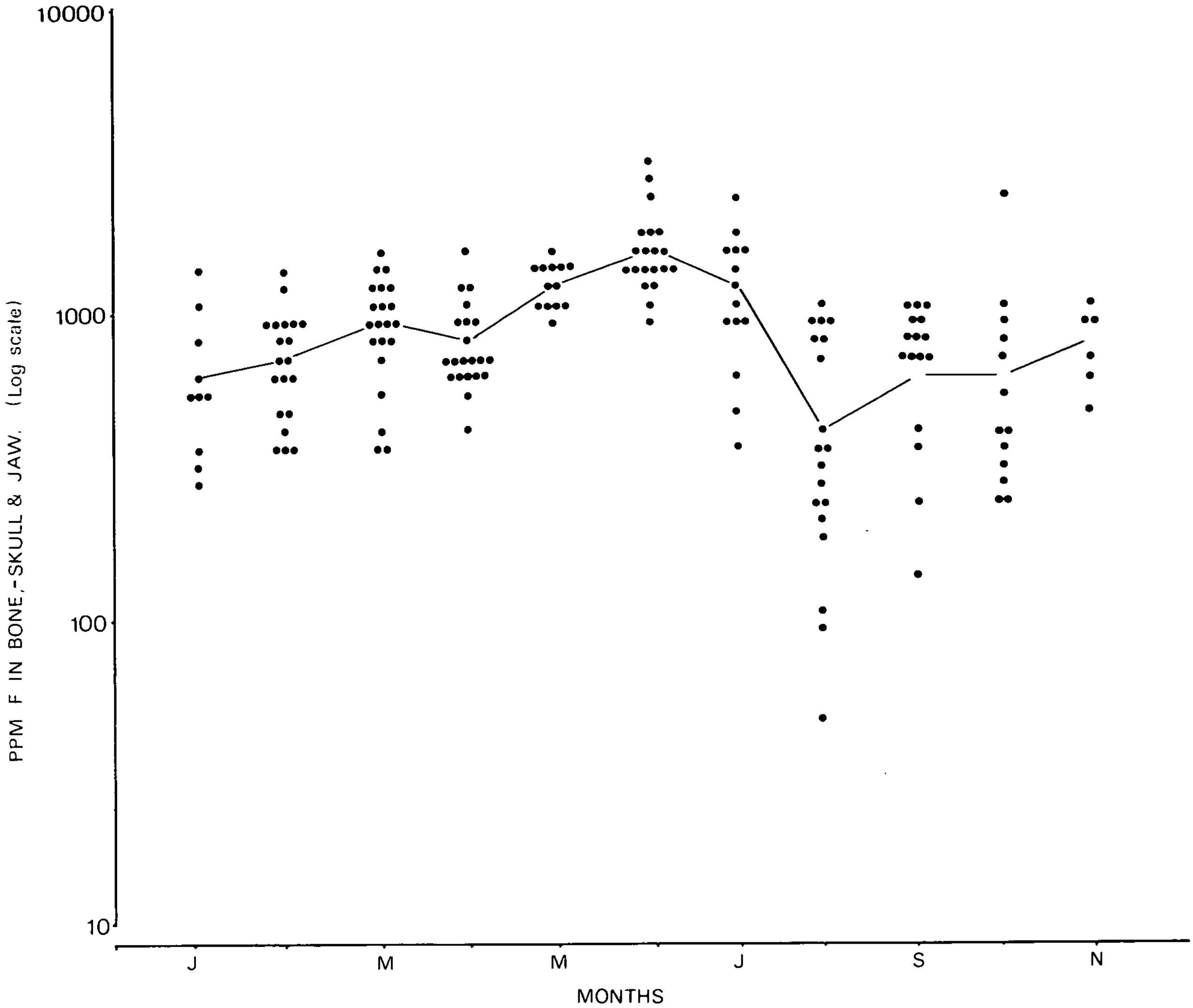

*Figure 14 Concentrations (ppm) of fluoride in skull and jaws of field voles (*Microtus agrestis*) trapped at monthly intervals, February 1979–January 1980, in a forest plantation 1 km south of the Anglesey smelter (lines are drawn between mean values).*

The second problem concerns the choice of bones. Some authors have suggested the femur, but, while this seems appropriate for mice and voles, it provides little material when working with shrews (*Sorex* sp). In the present study, measurements were made of different parts of the skeleton. While there were sometimes appreciable differences between the analyses of bones taken from different animals, the mean fluoride concentrations in vertebrae, ribs and long bones of field voles only differed by 13% from those of skull and jaws (Table 13).

Table 13. Comparison of mean fluoride concentrations (ppm) found in different bones of 2 groups of field voles (7 animals in each group)

	Type of bone analysed		
	Vertebrae, ribs, long bones, etc. A	Skull and jaws B	% difference between A & B
Group 1*	2200	1900	13
Group 2	9000	8000	13

*Voles sampled (1) 2 km and (2) 200 – 300 m from the smelter

The problem of interpretation is further exacerbated because fluoride tends to accumulate continuously in bones, and the amounts detected therefore reflect both the strength of local emissions and the periods of exposure, with young animals inevitably having smaller accumulations than old animals. Thus, Wright *et al.* (1978) reported mean fluoride concentrations of 2200 ppm in the femurs of adult field voles collected in May from a fluorspar tailings dam in Derbyshire, while Andrews *et al.* (1982) recorded 550 ppm in young voles collected from the same location in July.

Observations made during 1977 indicate that fluoride accumulation in field voles and wood mice is inversely related to the distance from the Holyhead smelter, with actual amounts ranging from 20–17 000 ppm and with 100–300 ppm being considered 'normal' in 'unpolluted' locations. To an extent, the latter concentrations are likely to reflect amounts of 'native' fluoride in soils. Although Wright *et al.* (1978) recorded 4400 ppm fluoride in femurs of *Apodemus sylvaticus* but only 2200 ppm in comparable tissues of *Microtus agrestis*, the specimens trapped during the present study had virtually identical accumulations. Notwithstanding the species difference at the Derbyshire site investigated by Wright and his colleagues, the bone accumulations in Derbyshire and Anglesey are of the same order, despite the much heavier accumulations of fluoride in soil and herbage at the former. As yet, this site effect remains unexplained, but it may be attributable to different sources of pollutant fluoride.

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MERSEY BIRD MORTALITIES 1979–1981: A POLLUTION PROBLEM RESOLVED?

(This work was largely supported by Nature Conservancy Council funds)

Osborn (1981) outlined some of the work being done to determine the cause of the mass bird deaths that occurred on the Mersey estuary (north-west England) in the late summer and autumn of 1979 and 1980. A fuller report is now given of the investigations.

Two lines of research were followed. First, sick, dead and apparently healthy birds were collected from the Mersey, and healthy birds were collected from other areas. Tissues from these birds were analysed for various toxic chemicals, including total lead and alkyl lead compounds. This work provided good evidence that the bird deaths had been caused by alkyl lead compounds, which probably originate from petrochemical industries on the Mersey (Head *et al.* 1980). Second, detailed observations were made of captive birds that had been exposed to alkyl lead compounds, and these observations confirmed the earlier suspicion that alkyl lead compounds could have caused the mass deaths that occurred on the Mersey.

Field studies

The 1979 mortality

In 1979, dead and dying birds were first observed on the estuary in mid-September. From then until early 1980, when the last few casualties were reported, about 2400 birds were known to have been affected, the great majority of which died. Details of the species affected can be found elsewhere (Head *et al.* 1980; Osborn 1981), but most casualties were waders, ducks or gulls. Half the recorded deaths were for one wader species, namely dunlin *(Calidris alpina).* Deaths of about 400 black-headed gulls *(Larus ridibundus)* were also recorded. It is not known what proportion the available figures represent of the true number of affected animals, as many carcases may have been lost to the river, taken by predators, or washed ashore in inaccessible or unsearched areas.

Most of the sick birds found were unable to fly and were unco-ordinated in their movements. Lack of feeding activity was also reported, and the waders involved, especially dunlin, exhibited a previously unrecorded head 'shiver'. The droppings, when dry, consisted of a white disk with a brilliant green centre.

Veterinary investigations by other laboratories have been summarised elsewhere (Head *et al.* 1980). None of the studies was able to attribute the deaths to any disease. Similarly, early post-mortems at Monks Wood eliminated the possibility that food shortage and subsequent starvation were the cause of death, as several of the birds found dead had died before their fat and protein reserves were exhausted. However, these post-mortems did show that affected birds had discoloured livers and brilliant green bile.

Toxic chemical analysis at Monks Wood showed that, whilst the birds contained very little, if any, residue of organochlorine compounds, mercury or cadmium, the lead levels were unusually high (Osborn 1981). Sick birds also had elevated levels of lead, and even healthy birds from the Mersey contained lead concentrations well above those found in birds on other estuaries (Figure 15). Furthermore, analysis at Monks Wood of tissues from sick and live Mersey birds suggested that they had been exposed to a relatively large acute dose of lead, because kidney levels were close to those in the liver and other soft tissues (see also Head *et al.* 1980). In chronic exposure, the kidney would be expected to accumulate much greater levels of lead than the liver.

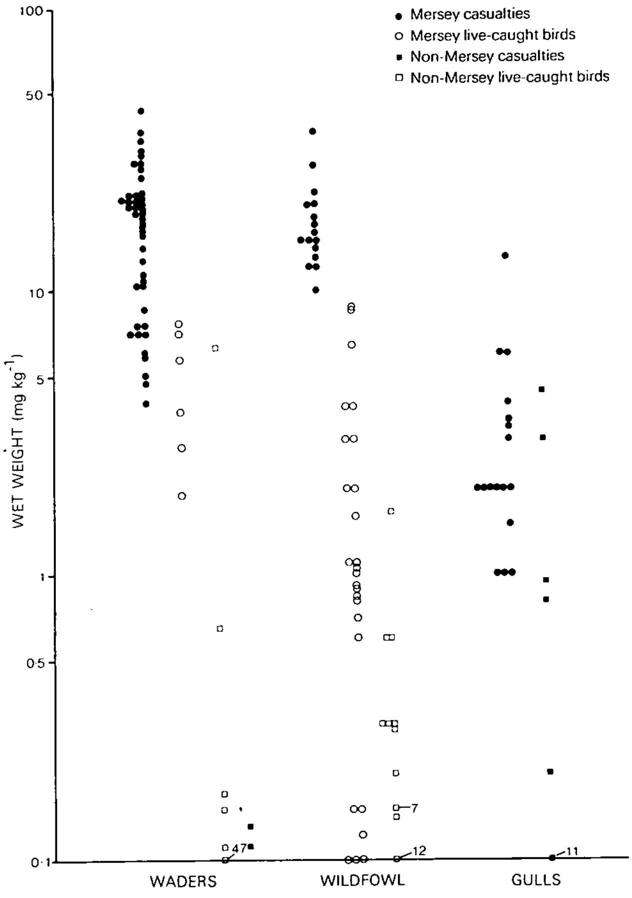

Figure 15 Liver lead levels mg kg^{-1} wet weight in waders, wildfowl and gulls from the Mersey and elsewhere: ● *Mersey casualties;* ○ *Mersey live-caught birds;* ■ Non-Mersey casualties; □ *Non-Mersey live-caught birds.*

Industrial analysts showed that 30–70% of the lead in the tissues was present in the form of alkyl lead compounds, mainly trimethyl lead. Later analyses at Monks Wood, using an anodic stripping voltammetric technique described on p. 91, confirmed this finding.

The 1980 mortality

At least 850 birds were found dead and dying in 1980 (for details, see Osborn 1981), but, in contrast to 1979, black-headed gulls were the major species involved. Unusually low numbers of dunlin seemed to be present at the time of the 1980 incident (see later). Because gulls were such predominant casualties in 1980, the North West Water Authority (NWWA), together with MAFF, investigated the possibility that the birds had died as a result of type C botulism, and 2 herring gulls *(Larus argentatus)* were confirmed to have the botulism toxin in their blood.

As in 1979, the waders and ducks affected in 1980 contained high levels of lead, much of which was in the form of alkyl lead compounds. Post-mortem findings once again indicated that affected birds had brilliant green bile, discoloured livers, and green-stained, or discoloured, intestines. It was also noted that affected birds had a distinctive odour.

1981 deaths

Very few dead and dying birds were reported in 1981. However, the behaviour of affected ducks and waders was similar to that seen in previous incidents. Post-mortem examination and chemical analysis also produced similar results: affected birds had discoloured livers, green bile, and the distinctive odour. Alkyl lead levels of up to 7 mg Pb kg^{-1} (wet weight) were found. Thus, it seemed that alkyl lead compounds were still seriously affecting some birds in autumn 1981.

Studies on apparently healthy birds

Figure 15 summarises the data available for live-caught birds. Many of those caught live in the Mersey estuary had higher lead levels than those found in birds from other places, much of it being in the alkyl form. Furthermore, the great majority of the waders and ducks with >1 mg kg^{-1} lead in their livers also had some of the post-mortem features (discoloured liver, green bile, distinctive odour, enlarged gall bladder) of birds found sick or dead on the Mersey.

Assuming that shooting apparently healthy birds introduces no bias into the sampling, then the implication is that many thousands of birds on the Mersey are at some risk from alkyl lead compounds. However, the total numbers of birds using the estuary do not appear to have been adversely affected by the 1979 and 1980 incidents (Table 14), although the number of redshank *(Tringa totanus)* and, possibly, the number of dunlin in the early part of the season do seem to be lower than in the pre-incident period. If there is a real risk to a large proportion of the birds using the estuary, a great deal of further field research would be needed to quantify the risk.

Several points raised by the field studies remain to be resolved, and await the results of the investigations by the North West Water Authority into the hydrodynamics of alkyl lead compounds in the water and biota of the

Table 14. Winter numbers of selected duck and wader species counted on the Mersey estuary: mean for 1971/77 (Buxton, unpublished) compared with numbers for 1980/81 and 1981/82 (G. Thomason *et al.*, pers. comm.)

		Sep	Oct	Nov	Dec	Jan	Feb	Mar
Mallard	1971/77	920	740	910	1350	1150	890	500
	1980/81	1250	1700	2400	1750	2400	1300	660
	1981/82	190	660	2300				
Teal	1971/77	2400	4200	6900	7100	7900	6100	3400
	1980/81	2500	7200	11000	18000	20000	26000	13000
	1981/82	5400	7300	9400				
Pintail	1971/77	1200	3300	6200	8500	7700	5300	1250
	1980/81	1950	130000	18500	8000	3900	12500	4000
	1981/82	260	4200	11500				
Shelduck	1971/77	180	360	700	1300	2300	2500	2600
	1980/81	1000	1300	8100	11000	9400	12000	3900
	1981/82	360	2200	12000				
Dunlin	1971/77	3900	11500	25000	23000	26000	25000	11500
	1980/81	63	10000	21000	40000	24000	31000	185000
	1981/82	720	7100	18000				
Redshank	1971/77	670	860	1400	960	1100	870	900
	1980/81	250	510	670	380	210	1050	600
	1981/82	98	780	550				
Curlew	1971/77	900	520	400	570	480	560	720
	1980/81	1250	430	490	91	440	500	880
	1981/82	810	780	390				

Note: Because of the potential danger to human health from eating contaminated wildfowl, wildfowling activities were restricted in 1979/80 and 1980/81. It has been suggested that the lack of shooting may have encouraged more birds than usual to overwinter on the Mersey in 1980/81.

estuary. It may then be possible to answer the following questions. What is the exact pathway by which the lead reached the birds? Why were mortalities, on the whole, restricted to late summer and autumn? Why, at least initially, were the mortalities associated with high tides? Why were there no noticeable mortalities prior to 1979, and why were they less severe in 1981?

Certainly, data available in the preliminary report from the Water Authority (Head *et al.* 1980) suggest that sufficient alkyl lead compounds enter the Mersey-Manchester Ship Canal system to account for the levels found. It is likely that prey items for the birds could easily accumulate enough lead from the water for toxic concentrations to occur in birds eating such contaminated prey (*Macoma* contained about 1 mg kg^{-1} lead, mostly alkyl lead compounds). The pathway, therefore, from the alkyl lead effluent outfalls to the birds seems easily explained.

Equally, recent reductions in alkyl lead effluent may explain why there were fewer mortalities in 1981.

However, the other questions raised above are more difficult to answer, and depend in part upon unravelling the complex hydrology of the Mersey-Manchester Ship Canal system. Probably, we shall never fully understand why mortalities were not seen before 1979. Ironically, it could be that, as the Mersey has become less polluted, the invertebrate and plant foods of these birds have increased, so attracting them to feed in contaminated areas which were previously avoided. If this is so, then the Mersey incident may be the first instance where a *general* decrease in pollution has led to increased wildlife mortalities, although, of course, the incident was caused by the continued presence of harmful quantities of a *specific* pollutant.

Experimental studies

Even though there may be extensive evidence from field studies to suggest that a particular toxic chemical might be causing a problem, the evidence, strictly speaking, is 'circumstantial' or 'correlative'. The possibility always exists, however remote, that an important environmental factor has not been measured, and that our conclusions would have been different had measurement of the 'missing factor' been included in the research programme. A laboratory-based experimental study overcomes some of the difficulties faced in the real world, enabling us, at least, to test hypotheses in controlled conditions.

Experimental studies were carried out in this investigation to test the hypothesis that alkyl lead had killed the Mersey birds and was placing a great many others at risk. For this hypothesis to be confirmed, alkyl lead compounds would have to be administered to birds, who would then have to exhibit behavioural phenomena similar to the affected Mersey birds, have the same internal lesions and abnormalities as affected birds, and contain similar amounts of lead.

Two experiments were performed with the 2 alkyl lead compounds with which the birds were most likely to come into contact, triethyl lead and trimethyl lead, the latter being the predominant form in the birds. Three different levels of treatment were given to starlings, a convenient and relatively well-known bird for laboratory work: 2 mg trialkyl lead chloride/day, 200 g trialkyl lead chloride/day, and 0 trialkyl lead chloride/day – the last, of course, being the control. It was hoped that such dosing with trialkyl lead would result in tissue levels close to those found on the Mersey. The higher dose was expected to be lethal in a short period of time, and the low dose was expected to help determine the 'no effect' level of trialkyl lead compounds in birds.

Dosing was ended after 11 doses and birds were examined to see whether their internal morphology had been in any way affected by the treatment. Also, various measures of body condition were taken, eg weight of muscles, liver and kidney, size of fat reserves, etc. During the course of the experiment, the birds had been observed in order to compare their gross behaviour with that of birds on the Mersey, and their daily food consumption had been measured.

Experimental results

1. Tissue levels of trialkyl lead in the high- and low-dose laboratory starlings were similar to those found in substantial numbers of birds on the Mersey in the autumn and late summer periods (Table 15, Figure 15).
2. Morphological changes in the laboratory birds were similar to those found in Mersey birds containing similar levels of trialkyl lead compounds (Table 16), eg green-stained livers, discoloured intestines, enlarged gall bladders. In the trimethyl lead experiment, all the low dose birds had the same characteristic odour found in the Mersey casualties, but fewer birds had this odour in the triethyl lead experiments. In addition, some activation of bone marrow was observed.

   The results suggest that the presence of trialkyl lead compounds cause a number of characteristic internal lesions, all probably deleterious to the animal's welfare. The internal morphological changes to the enterohepatic system may be 'diagnostic' of trialkyl lead poisoning. They do not seem so apparent in inorganic lead poisoning.

Table 15. Trialkyl lead levels (as mg Pb kg^{-1} wet weight) in tissues of dosed starlings

Details	Mean	SE	Range
Triethyl lead experiment			
Low dose starlings			
Muscle	1·47	0·36	0·4–2·9
Liver	1·07	0·2	0·6–1·9
Kidney	1·85	0·17	1·4–2·5
Bone	0·19	0·02	0·1–0·3
Brain	0·54	0·04	0·4–0·7
High dose starlings			
Muscle	20·0	2·78	9·5–30·0
Liver	40·2	9·35	14·6–92·3
Kidney	19·9	3·22	9·9–28·7
Bone	6·0	1·59	1·4–9·6
Brain	7·3	1·27	3·8–12·3
Trimethyl lead experiment			
Low dose starlings			
Muscle	3·07	0·55	1·6–5·3
Liver	3·70	0·56	2·1–5·6
Kidney	5·38	0·88	2·8–8·0
Bone	0·39	0·12	0·1–0·9
Brain	3·50	0·79	1·3–6·6
High dose starlings			
Muscle	11·0	2·20	6·1–19·4
Liver	32·4	4·93	18·5–49·7
Kidney	30·2	6·21	17·0–57·3
Bone	4·3	1·14	0·2–8·5
Brain	16·7	2·65	10·0–26·7

Levels in control birds were less than 0·1 in all cases.
Low dose = 200 μg day^{-1} PbR_3Cl
High dose = 2 mg day^{-1} PbR_3Cl

3. Behavioural changes in the laboratory starlings are difficult to compare with birds in the wild, but some comparisons can be made. The low dose birds all retained the capacity to fly in the triethyl experiment, and all low dose birds in the trimethyl experiment flew apparently normally. The high dose birds in the triethyl experiment became very quiet and fluffed their feathers as if cold. However, some flew briefly until just before death, which was sudden and unheralded by anything but the mildest 'symptoms', although this may not be uncommon in birds.

   The trimethyl high dose birds exhibited a syndrome so disturbing that 4 of the 6 experimental birds

Table 16. Scores of morphological changes in trialkyl lead dosed starlings. Figures are sum of scores for all 6 birds in the group. The range of individual scores is in parentheses

	Gall bladder		Bone		Gut		Muscle	
	Triethyl	Trimethyl	Triethyl	Trimethyl	Triethyl	Trimethyl	Triethyl	Trimethyl
Controls	0	3·5(1–1·5)	0	9·5(1–2·5)	0	0	–	17·25(2·5–3)
Low dose	12(2–2)	14·5(2–3)	6(1–1)	11·5(1–2·5)	1(0–1)	7(1–2)	–	12·5(1·5–2·5)
High dose	21(3–4)	22(2–4)	20(2–4)	17(1–4)	3(1–2)	16(1–4)	–	0

Gall bladder score is for enlargement; bone score is for redness of marrow; gut score is for discoloration; muscle score is for 'condition' or 'quantity/quality' of muscle

Except for muscle: 0 = normal; 4 = greatly different from normal
For muscle: 0 = wasted; 4 = best possible condition

had to be killed. This syndrome consisted of head tremors, some shivering, inability to perch, and severe disorientation. These birds could not have flown. Green droppings were seen in some low dose birds in both experiments, and in many of the high dose birds. The trimethyl birds' droppings were more like those of the affected Mersey animals. These behaviour observations add to the view that trialkyl lead compounds caused the Mersey bird mortalities.

4. Feeding records during both of the experiments were interesting in that they revealed that birds dosed with trialkyl lead compounds had disrupted feeding patterns, in comparison with control birds (Figure 16). This effect is of considerable importance for wild birds whose food supply is less certain.

5. Physiological measurements were taken mainly to help determine the 'no effect' level of trialkyl lead, below which birds would be virtually unaffected, and above which they would be subject to serious, if sublethal, effects.

Table 17. Measures of body condition in starlings (means± SE; n = 6; range shown for lipid values)

	Lean dry body weight (g)	Pectoral muscle (g)	Body lipid (g)	Intramuscular fat (g)
Triethyl experiment				
Controls	21·5 ±0·7	1·88 ±0·08	2·92 (2–5)	0·10 (0·04–0·13)
Low dose	21·5 ±1·0	1·85 ±0·14	1·72** (0·7–2·4)	0·05 (0·02–0·08)
High dose	17·7*±0·3	1·25*±0·05	0·39*	0·05*
Trimethyl experiment				
Controls	20·5 ±0·8 (21·3 ±0·3)	1·98 ±0·07 (2·03 ±0·07)	4·5 (5) (2–7·5)	0·16 (0·18) (0·05–0·22)
Low dose	19·7 ±0·4	1·75*±0·09	4·3 (2–11·5)	0·13 (0·06–0·3)
High dose	17·9*±0·7	1·26*±0·12	2·3 (0·5–11)	0·02* (0–0·13)

*Means so marked are significantly different (P<0·05) from controls; Student's t test
** Significantly different if corrected for body size
In the trimethyl experiment, one of the controls was deformed. The figures in parentheses are the means without this bird included.

In birds, there are 2 important measures of physiological condition which are of great significance for breeding, survival, and migration, ie the levels of fat and protein reserves. Indices of these levels are provided by determining the bird's total fat content and by the weight of the pectoral muscles; Table 17 presents the results. In both experiments, these measures were much reduced in the high dose birds, and some reduction was also observed in the low dose birds. The most marked effect in the low dose groups was the reduction in muscle weight that occurred in the trimethyl experiment, which was probably first evident after 6 doses.

An additional useful measure of physiological function is organ weight, particularly of the liver and kidney. It was found that kidney weight was reduced in the high dose trimethyl group and liver weight was increased in the low dose trimethyl group. (The liver often enlarges in the presence of a toxic chemical.) No clear effects on liver or kidney weight were seen in the triethyl experiment.

The physiological observations suggest that, even at quite low levels, trialkyl lead compounds can adversely affect the physiology of birds in such a way as to

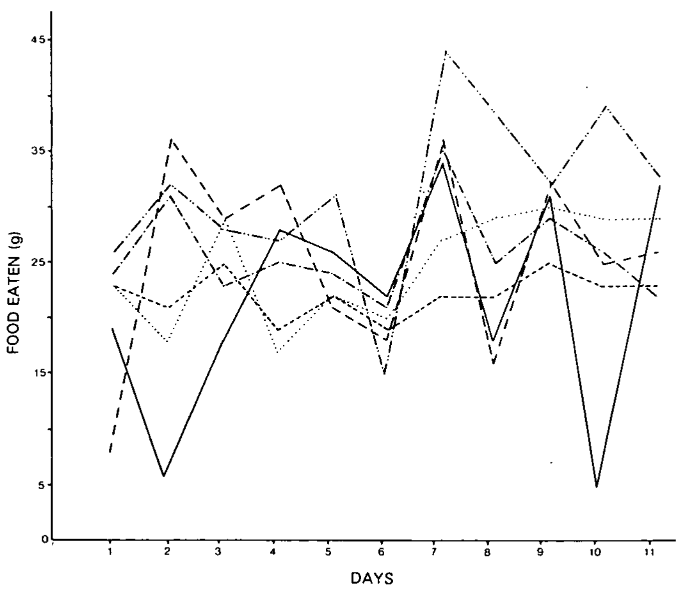

Figure 16 a. Daily food consumption in starlings receiving 200 µg trimethyl lead chloride per day.

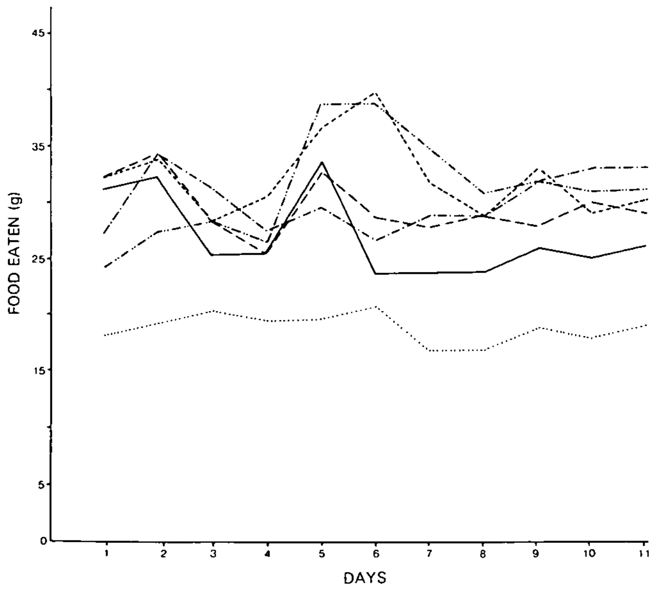

Figure 16 b. Daily food consumption in control starlings.

additionally 'stress' the bird, or reduce its chances of survival directly.

Experimental conclusions
Trimethyl and triethyl lead compounds kill laboratory birds, when tissue levels are similar to those found in dead birds on the Mersey. At levels insufficient to cause death, physiology and internal morphology are affected in ways likely to reduce survival, or to make an animal less able to deal successfully with 'stress', such as food shortage, bad weather, or disease. These sublethal effects may begin when concentrations in liver, muscle, kidney or brain reach 0·5–1 μg Pb per gram of tissue (on a wet weight basis).

Conclusions
1. Dead, sick and live birds from the Mersey contain elevated levels of lead in their tissues, compared with those on other estuaries, most of which is in the trialkyl form. Birds killed with alkyl lead compounds in dosing experiments contained similar amounts of lead to the levels found in dead Mersey birds. In addition, the behaviour and internal features of dosed birds were similar to those of dead and sick Mersey birds.

2. We conclude that the death of birds on the Mersey was primarily the result of contamination of the environment with alkyl lead compounds (see also Head *et al.* 1980), assuming, of course, that waders and ducks do not respond to lead poisoning very differently from starlings.

3. The experimental results also suggest that birds containing more than 0·5 mg Pb kg^{-1} (wet weight) as alkyl lead have changed internal and physiological features which will reduce their survival prospects. As many Mersey birds contain this amount of alkyl lead, and as such birds often have some internal features similar to those in both the experimental birds and the sick Mersey birds, it seems reasonable to conclude that many of the thousands of birds using the Mersey estuary – one of Britain's most important overwintering grounds for ducks and waders – may be at some risk from the sublethal levels of alkyl lead compounds they contain.

4. Monitoring of alkyl lead compounds in the Mersey areas should continue until acceptable concentrations have been reached in water and biota.

D. Osborn and K. R. Bull

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MONITORING FOR THE EFFECTS OF POLLUTANTS

(This work was largely supported by Department of Environment funds)

Work ended this summer on a 2-year contract with the Department of Environment, to review monitoring within Great Britain for the biological effects of pollutants. Although pollutants act on individual organisms, it is the impact on populations that is important, apart from man and his cultivated and domesticated species. Deaths of individuals do not necessarily affect the population, because high death rates may be offset by improved survival of the remainder.

In general, pollutants may affect populations in 3 ways, each of which can be monitored.

1. They may change the population size, structure (eg age distribution, sex ratio) or distribution, and, in extreme cases, of course, the population may disappear completely. It must be remembered, however, that many other factors besides pollution will continually affect these aspects of populations.

2. They may change the gene pool, as in the spread through a pest population of genes resistant to one or more pesticides.

3. They may change the structure and performance of individuals, of which the classic example is egg-shell thinning in birds and the consequent reduced breeding rate.

Many monitoring schemes exist in Great Britain, and, although criticisms of detail can be made, these schemes will detect significant changes occurring in our flora and fauna. However, it is usually difficult to identify the cause of any biological changes, and the most that can be expected is correlation between observed changes in distribution, numbers or population structure, and changes in environmental factors, such as amounts of pollutant, food supply or weather, when these have been measured. The difficulty of identifying causes was demonstrated by the decline of egg-shell thickness, first observed in the peregrine falcon (*Falco peregrinus*) by Ratcliffe in 1963, and now, after much observation, experimental work and controversy, generally accepted to result from the use of p,p'-DDT.

In addition, plants or animals can be analysed for their pollutant content. Such analyses may indicate the likelihood of biological effects, or be used to measure the distribution, and changes with time, of amounts of pollutant in the environment. However, this type of information alone gives no direct indication of the impact of pollutants on populations.

If the degree of environmental contamination by chemical is to be measured, plants and animals are not usually the best material for analysis. Samples of air, soil, water, sediments or other abiotic material should, in properly designed programmes, give more useful information about the degree of environmental contamination. Plants and animals introduce additional variability into the results of chemical analyses, and are to be preferred only when analysis of abiotic samples is technically difficult. The only other good reasons for analysing amounts of pollutants in organisms are to indicate the likelihood of biological effects on that species, or as an intermediary for biological effects in other species, particularly as a source of pollutants in food for man.

Scientifically, the design of effective monitoring programmes poses some interesting problems that deserve investigation. Obviously, the design of any monitoring programme should be influenced by its objectives, and different programmes may have different objectives.

Pollution only occurs when contaminants have biological effects, particularly effects on populations, and proof of such effect is difficult. Not only are the relationships complex between effects on individuals and the consequences for populations, but populations fluctuate in size from many causes besides potential pollutants.

For persistent pollutants, amounts within organisms are commonly measured to indicate the likelihood of biological effects, but there is little evidence of the nature of the relationship between exposure and the degree of biological effect in field conditions. Ideally, the mass or concentration of pollutant at the site of action should be measured within the animal, but the site of action is often unknown and, if known, the amounts of pollutant present are likely to be below the analytical limits of detection. It is commonly assumed that the degree, or likelihood, of effect increases with amount of pollutant, and that there is a threshold dose below which there is no effect.

In practice, dose is usually measured as the mass or concentration of pollutant in the immediate environment, as the amount ingested or otherwise taken into the body, or as the amount in a specific tissue or organ, preferably the critical organ. Current work on SO_2 favours the estimate of dose as flux rate through the plant's stomata integrated over the exposure period. Such measures are certainly useful for short-term acute effects: they are the essence of estimates for LD_{50}s and similar bioassays. Their usefulness for long-term sublethal exposures is much less certain, when the amount of pollutant retained by the organisms may be only a small proportion of the amount absorbed: the greater part of the pollutant may have been metabolised and/or excreted. One may reasonably expect such measures of dose to relate to biological effects, if the conditions of exposure are constant, and if the organism's sensitivity to the pollutant remains constant, but both these assumptions are seldom valid in field conditions. It is true that, for a few organochlorine insecticides, it is possible to define a critical concentration in the liver, and that the degree of shell thinning in birds correlates reasonably well with the amount of p,p'-DDE in the egg, but, in both these examples, the biological response, ie death or the laying of eggs with thin shells, occurs quite rapidly, and can be regarded as instances of acute poisoning. They do not affect the main argument.

The inadequacy of conventional measures of dose was appreciated for radionuclides, when the 'dose commitment' of human populations was calculated for proposed nuclear explosions. The incidence of cancer is assumed to be directly proportional to the integral of mass or concentration of radionuclide present within the body, plotted against the duration of exposure. Similar calculations are being made for other potential pollutants, and for other species. For most pollutants, there is an untested, and perhaps unlikely, assumption that degree or likelihood of effect is proportional to the product of mass present and time, and that, in general, neither the duration nor the rate of exposure is important *per se*, with no threshold for either duration or intensity of exposure. All stages of the life cycle are also assumed to be equally sensitive, which is demonstrably untrue for at least some animals and plants.

There is little or no information on the relationship between levels of pollutants in specific tissues during fluctuating exposures, and the consequent chronic biological effects. Results of chemical analyses for amounts of pollutant in effluent, or in the environment, are sometimes expressed as the percentage of occasions on which certain values are exceeded. This can be a useful way of expressing results, but it raises the question as to whether infrequent relatively high exposures have significant biological effects.

Given these difficulties of interpretation, the best monitoring method, though at present untested, may be to measure the effect of a pollutant on a population's gene pool. Melanism provides a good example, where the impact of air pollution, principally particulates and SO_2, on the moth *Biston betularia* can be measured by the proportion of melanic moths in the population. Neither the population size nor its boundaries need to be known, but account should be taken of differences between populations. Suppose, for example, that one population of *B. betularia*, with a significant degree of adult predation by birds, were exposed to a sufficient level of particulates and SO_2 for the population to consist predominantly of melanic individuals. Another population of *B. betularia* exposed to the same level of particulates and SO_2, but with an insignificant degree of predation by birds, could well retain the typical coloration. The incidence of melanism would indicate the degree of effect from air pollution, but would be a poor measure of the amount of air contamination, because of the other variable involved, namely predation. This particular example has the added attraction that monitoring could possibly be done mostly by amateurs. However, in general, the effect of pollutants on gene pools that should be measured, by laboratory tests on samples taken from populations in the wild, is the resistance (tolerance) of different populations to that contaminant. SO_2 and flowering plants, or heavy metals and benthic organisms in aquatic habitats appear to be the obvious combinations with which to test this approach. If resistance develops in one species, there is a *prima facie* case to suggest that populations of some other species, more or equally susceptible and less able to evolve resistance, have also been affected. Research has been started to test these ideas.

F. Moriarty

ECOLOGY, 'EPIDEMIOLOGY' AND EFFECTS OF SOME SHEATHING (ECTO-)MYCORRHIZAL ASSOCIATIONS

The value of sheathing mycorrhizas was clearly seen when Central American pines were introduced into West African countries in the 1930s (Momoh & Gbadegesin 1980). Without the benefit of mycorrhizal inocula contained in Central American soils, these pines failed within 18 months, but have become successfully established in West Africa, after the subsequent introduction of soils and the formation of sheathing mycorrhizas. Despite this important effect, few other observations have been made in the forest of the effects of sheathing mycorrhizas on the macroscopic growth of trees, with the notable exception of those made by Dr D. H. Marx and his team in Athens, Georgia, USA.

Where field experiments have been made, much of the interest in sheathing mycorrhizas has centred on the use of (i) infested soils, (ii) needle litter, and (iii) spores and sporophore tissues. However, bearing in mind the benefits to be gained from the use of identifiable isolates of the root nodule bacterium *Rhizobium trifolii*, when maximising nitrogen fixation in legumes, it would seem appropriate to investigate a more exacting approach to the selection of mycorrhizal inocula, ie the use of 'selected' isolates. Without an adequate knowledge of the ecology and epidemiology of mycorrhizal fungi, however, it has not been possible to adopt a rational approach to possible inoculation procedures. This article reviews recent work in northern Britain by ITE staff concerned with the ecology of fungi forming sheathing mycorrhizas with native birches (*Betula* spp), and the introduced Sitka spruce and lodgepole pine. The team has also followed seasonal changes (epidemiology) and effects on host survival and growth.

Occurrence of fruitbodies of mycorrhizal fungi and the concept of succession

During the past 5 years or more, the production of mycorrhizal fruitbodies, usually in the autumn, has been shown to be over-ridingly influenced by host factors. In mixtures of *Pinus* spp, *Betula* spp, *Alnus* spp and *Sorbus aucuparia*, the fruitbodies of *Suillus luteus* (slippery Jack) were associated with *Pinus* spp, and those of *Hebeloma crustuliniforme* (poison pie) and *Laccaria* (see footnote) with birches, whereas the fruitbodies of *Paxillus involutus* (brown roll rim) and the earth-fans of *Thelephora terrestris* were more or less equally abundant around trees of all species observed.

While toadstools of *Hebeloma crustuliniforme* and *Laccaria* are associated with birch seedlings and saplings (Mason *et al.* 1982) (Figure 17), fruitbodies of species of *Amanita* and *Russula*, which also form mycorrhizas, are commonly found near old specimens of *Betula* spp (Pegler 1981). There is, therefore, evidence to suggest that the production of mycorrhizal fruitbodies follows a highly ordered pattern, a notion confirmed by the successive appearance of *Inocybe lanuginella*, other species of *Hebeloma*, *Lactarius pubescens*, *Leccinum scabrum* (brown birch bolete), *Leccinum roseofractum* and species of *Cortinarius* (Figure 18).

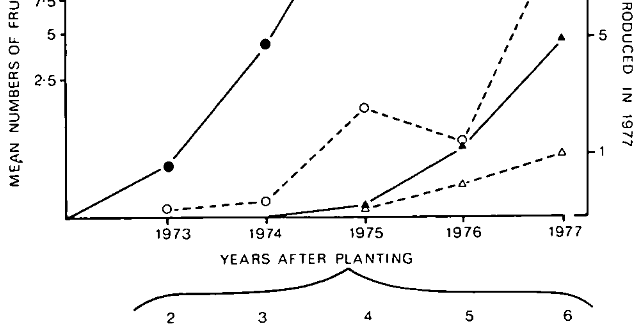

Figure 17 Numbers of autumnal fruitbodies of 4 genera of fungi associated between 1973 and 1977 with birch saplings planted in 1971. ● Hebeloma; ○ Laccaria; ▲ Inocybe; Δ Lactarius *(Mason* et al. *1982).*

Footnote: Our original identification of *Laccaria laccata* needs to be corrected as most of the specimens recently examined have 2-spored basidia, characteristic of *L. ohiensis* and *L. tortilis*, instead of 4-spored basidia typical of *L. laccata*

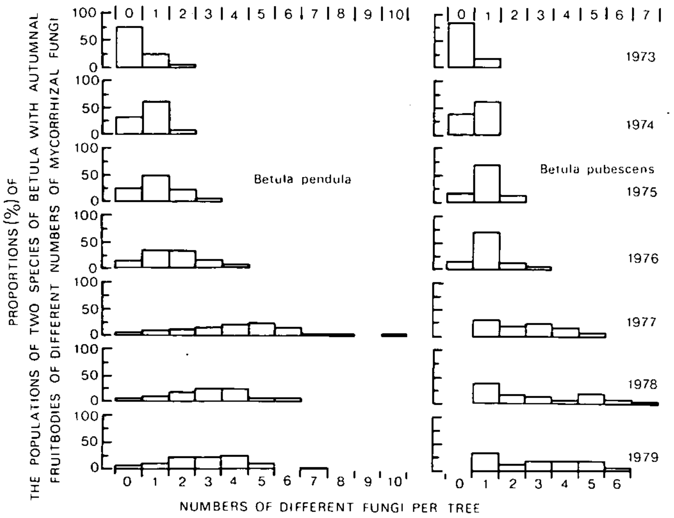

Figure 18 Number of different fungi, producing readily observable autumnal fruitbodies, associated with populations of Betula pendula *and* B. pubescens *in successive years after planting saplings in 1971 (Mason* et al. *1982).*

However, what is the relationship between above-ground fruitbodies and subterranean mycorrhizas? Does the succession of fruitbodies reflect the sequential development of different types of mycorrhizas? Qualitative studies by Warcup have shown that fruitbodies are closely associated with mycorrhizas formed by the same fungus. With this reassurance, but accepting that the presence of mycorrhizas formed by non-fruiting fungi cannot be precluded, experiments are investigating the abilities of early- and late-stage fungi to establish mycorrhizas in field crops when subject to competition from the gamut of soil microbes (Figure 19).

Production of seedlings with sheathing mycorrhizas

To minimise risks of contamination, a closed system was designed using horticultural seed trays fitted with transparent (propagator) lids (Mason *et al.* in press). Prior to sterilisation by gamma radiation, each tray is packed with 140-150 grey polystyrene tubes as supplied to the Forestry Commission by Telcon Plastics, Orpington, Kent. The tubes, which are split and measure 50 mm by 13 mm (diameter) after shortening, are filled with a nutrient-amended vermiculite/peat substrate suiting the growth of both tree seedlings and mycorrhizal fungi. After sterilising, each tube is planted with one microbe-free seedling grown from seeds surface-sterilised with hydrogen peroxide. The seedlings are incubated at 20°C in continuous light until mycorrhizas are well established, usually 8 weeks.

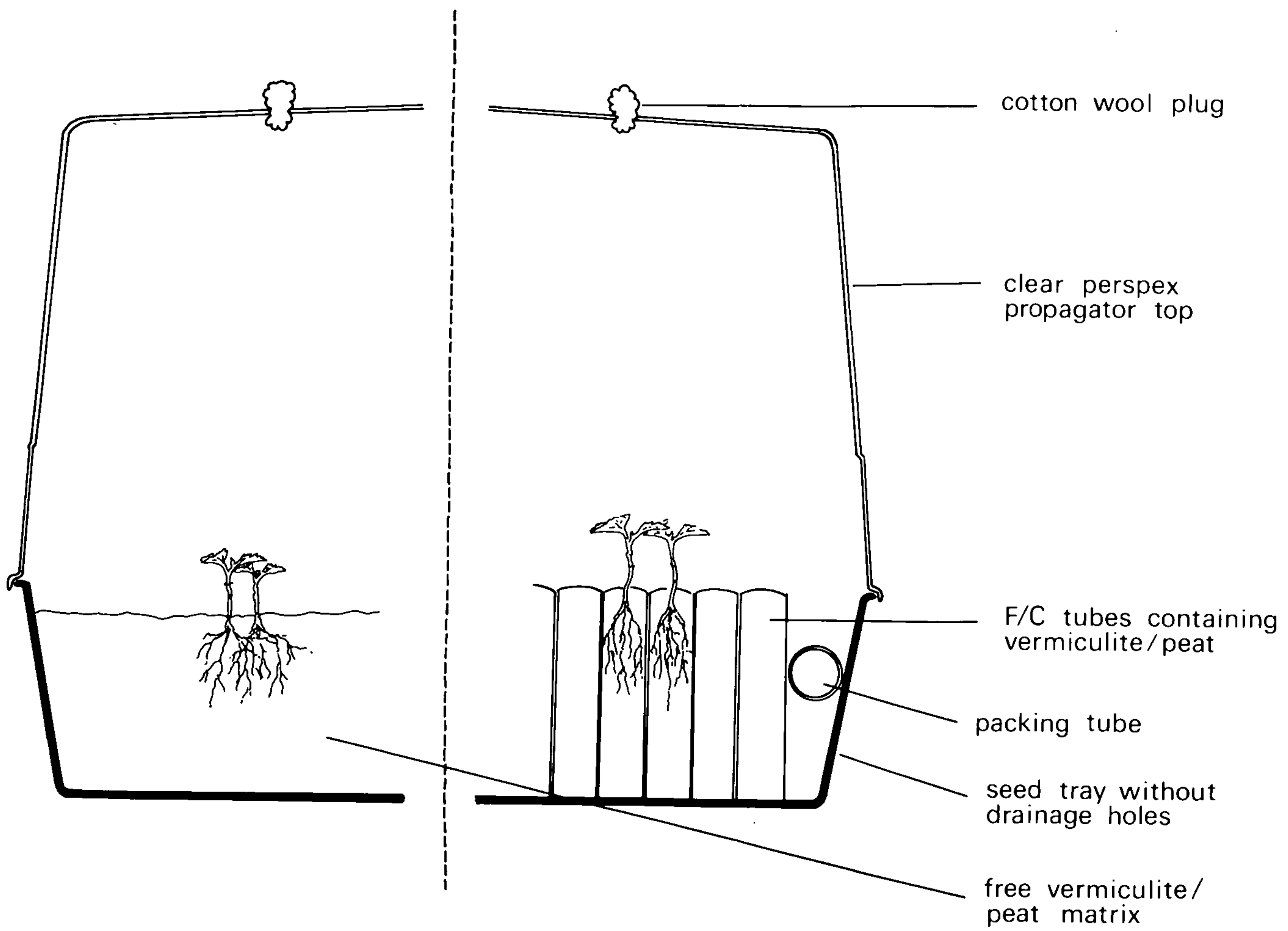

Figure 19 Closed system for establishing sheathing mycorrhizas during propagation. On right, seedlings grown in tubes 50 mm × 13 mm (internal diameter); on left, seedlings not grown in tubes. (F/C, Forestry Commission) (Mason et al. *in press).*

Thereafter, seedlings are hardened off, before being planted into field soils which have not been sterilised. Not surprisingly, colonization by mycorrhizal fungi has a profound effect on developing systems of roots, the effects being greater when seedlings were grown in tubes than when seedlings were growing 'freely' in substrates in relatively spacious flasks. Confinement in tubes increased the proportion of roots forming mycorrhizas, and these roots were also longer and more branched when *Amanita muscaria* (fly agaric) isolate 71 was used, but not when isolate 141 was employed (Mason *et al.* in press).

Although most trees are transplanted bare-rooted, the method of inoculating with sheathing mycorrhizal fungi is well suited to the production of container-grown seedlings, and has now been used successfully for propagating pine and spruce seedlings with an array of mycorrhizal fungi.

Interest in fruitbody succession triggered an experiment in which *Betula pendula* seedlings were inoculated, while being propagated in 'tubes', with *Hebeloma sacchariolens* or *Paxillus involutus* (both 'early' fungi) or *Amanita muscaria* (a 'late' fungus), prior to being transplanted into pots containing peat or 2 mineral soils.

At the end of propagation, at least 65% of the roots of all inoculated plants had mycorrhizas. However, by day 17 after planting, only 35% of roots of seedlings inoculated with *Amanita muscaria* were mycorrhizal (Table 18). The inability of this 'late' stage fungus to spread and infect roots newly developing in unsterile soils was confirmed 104 days later, when less than 1% of roots were colonized by *Amanita muscaria*, but, as in the uninoculated controls, approximately 30% of roots had mycorrhizas, the balance being attributable to *Thelephora terrestris*, *Laccaria proxima* and *Inocybe lanuginella* presumably occurring naturally in the different soils.

In contrast to *A. muscaria*, the 2 'early' stage fungi, *Hebeloma sacchariolens* and *Paxillus involutus*, both spread to form mycorrhizas on 45% and 51% of roots by day 121. Although many roots remained non-mycorrhizal on plants inoculated with these 2 fungi, infections were not formed by inocula naturally occurring in the unsterile soils. Thus, it seems that both 'early' and 'late' fungi can form mycorrhizas in sterile conditions, but only the former succeed on seedlings growing in unsterile substrates.

Because of the existing literature, it would be foolish to ignore the effects of soil nutrients on the establishment of mycorrhizas, a problem possibly exacerbated by the relative fertility of forest nurseries compared with forest soils. In general, mycorrhizas seem to develop more profusely on trees growing on nutrient-poor soils than on those in fertile substrates, but do all host/fungus combinations respond similarly? When seedlings of lodgepole pine (*Pinus contorta*) were grown with large amounts, 1·50 kg m^{-3}, of a complete fertilizer, the formation of sheathing mycorrhizas by *Hebeloma sacchariolens* and *Paxillus involutus* was inhibited (Table 19). However, the responses differed appreciably with smaller amounts of fertilizer, mycorrhizal development with *Paxillus involutus* being greater with 0·75 kg than with 0·13 kg m^{-3}, whereas the opposite was true of *Hebeloma sacchariolens*.

Table 19. Effects of different amounts of a complete (NPK) fertilizer on the formation of sheathing mycorrhizas when seedlings of *Pinus contorta*, growing in paper pots, were inoculated with either *Hebeloma sacchariolens* or *Paxillus involutus*.

Amounts of fertilizer	Uninoculated controls	Seedlings inoculated with *H. sacchariolens*	Seedlings inoculated with *P. involutus*
0·13 kg m^{-3}	<1%*	55%	19%
0·75 kg m^{-3}	<1%	16%	50%
1·50 kg m^{-3}	Nil	<1%	<1%

*Proportion of root tips that were mycorrhizal

Effects of sheathing mycorrhizas on the growth and establishment of trees

Studies of the effects of sheathing mycorrhizas have been focused on nutrient uptake. However, recent experiments with birch and *Amanita muscaria* showed

Table 18. Effects, on percentages of root fragments that developed mycorrhizas, of inoculating seedlings of *Betula pendula* with different mycorrhizal fungi during propagation (mean effects in 4 soils; total numbers of root fragments with mycorrhizas as % of total number of root fragments counted).

Sampling dates	Uninoculated control	Inoculated during propagation with: *Hebeloma sacchariolens*	*Paxillus involutus*	*Amanita muscaria*	LSD (P = 0·05)
At planting	Nil	82·1%	88·5%	65·8%	
		(65·0) +	*(70·2)*	*(54·2)*	*(8·75)*
17 days after planting	Nil	45·3%	85·7%	35·4%	
		(42·3)	*(67·8)*	*(36·5)*	*(7·49)*
79 days after planting	1·5%	8·8%	29·6%	2·0%	
	(7·0)	*(17·3)*	*(33·0)*	*(8·2)*	*(5·61)*
121 days after planting	31·3%	45·1%	51·0%	29·3%	
	(34·4)	*(42·2)*	*(45·6)*	*(32·8)*	*(8·63)*

+ For analyses, percentages were transformed to angles which are italicised that the relative balance of stem tissues was significantly altered after the formation of mycorrhizas. Instead of an epidermis one cell thick, the formation of mycorrhizas triggered the seemingly premature development of a multi-layered epidermis and the evolution of a cortex with many intercellular airspaces, changes comparable to those in the tomato following root colonization by endomycorrhizal fungi (Daft & Okusanya 1973).

These changes could be important; the accelerated development of bark may increase the tolerance of trees to drought, whereas the development of intercellular airspaces is an adaptation found in plants capable of tolerating wet, waterlogged conditions. An experiment started with Sitka spruce (*Picea sitchensis*) in May 1981, with Dr C. Walker of the Forestry Commission, is already indicating the benefits to be gained by controlled 'mycorrhizal' inoculations. Seedlings were inoculated during propagation with isolates 0086 or 16 of *Paxillus involutus* or *Laccaria 'laccata'* and then transplanted into 4 different soils, 2 peats and 2 mineral soils. Within 5 months, the 'inoculated' seedlings were significantly taller than their uninoculated controls, isolates 0086 and 16 of *P. involutus* increasing heights by 18% and 61%, whereas *L. 'laccata'* more than doubled growth from 3·1 cm to 6·7 cm. Interestingly, these effects reflect the influences of the different isolates on mycorrhizal development, *P. involutus* isolate 0086 inducing fewest mycorrhizas and *L. 'laccata'* the most (Plate 1).

Effects of this magnitude would be of great importance if they were to be repeated in forest practice. They need to be confirmed in field conditions and in comparison with seedlings colonized by naturally occurring inocula. The effects of different isolates of *Paxillus involutus* differ significantly. How about those of different isolates of *L. 'laccata'*? Should other 'early' stage fungi be screened? Could it be that the effects observed are really attributable to the massive amounts of inocula? Is the variation among isolates of mycorrhizal fungi matched by comparable variation among seedlots of Sitka spruce? Is the host/fungus relationship significantly altered by soil conditions, in addition to the effects of available nutrients already mentioned? There are many questions to be answered, for which the need will intensify as our observations lend support to the work of Marx (1975) and his associates who attempted to improve establishment and subsequent growth of trees on heaps of industrial spoil.

Marx has focused attention on the benefits derived from inoculations with *Pisolithus tinctorius*, a yellow-brown gasteromycete closely related to *Scleroderma* spp (the earth balls) and found in many parts of the world, but only once recorded in Britain (Marx 1977). Our efforts have been devoted to local, indigenous, fungi, some of which confer considerable benefits on their hosts. In more than one experiment, we have found that the survival of birch seedlings planted into coal spoil was greatly improved by inoculation, during propagation, with isolates of *Hebeloma sacchariolens* and *Paxillus involutus* (Table 20), effects parallelled to some extent by those on the height growth of the survivors (Table 21).

In recent years, interest in sheathing mycorrhizas has been rekindled. Can plant growth be improved by replacing mycorrhizas formed by natural inocula with mycorrhizas formed by controlled inoculations of selected, 'superior' isolates? The probability of success may be enhanced by taking heed of the sequence of

Table 20. Effects on survival, after transplanting into 3 different substrates, of inoculating seedlings of *Betula pendula* during propagation with different sheathing mycorrhizal fungi.

Inoculation treatments	Unsterile substrates: Agricultural soil pH 5·7	Coal spoil: pH 5·5	Coal spoil: pH 3·9	Means on spoil
A. Survivors of 48 plants, 3 weeks after transplanting				
Uninoculated control	45	42	43	42·5
Inoculated with:				
(i) *Hebeloma sacchariolens* strain 4	41	48	48	48·0
(ii) *Paxillus involutus* strain 3	41	48	48	48·0
(III) *Paxillus involutus* strain 16	40	48	48	48·0
B. Survivors of 24 plants, 55 weeks after transplanting				
Uninoculated control	17	11	0	5·5
Inoculated with:				
(i) *Hebeloma sacchariolens* strain 4	24	24	23	23·5
(ii) *Paxillus involutus* strain 3	24	24	22	23·0
(iii) *Paxillus involutus* strain 16	24	24	24	24·0

Table 21. Effects on height (cm), after transplanting into 3 different substrates, of inoculating seedings of *Betula pendula* during propagation with different sheathing mycorrhizal fungi.

	Unsterile substrates			
		Coal spoil		
Inoculation treatments	Agricultural soil pH 5·7	pH 5·5	pH 3·9	Means on spoil
A. 3 weeks after transplanting				
Uninoculated control	12	10	7	8·5
Inoculated with:				
(i) *Hebeloma sacchariolens* strain 4	11	21	14	17·5
(ii) *Paxillus involutus* strain 3	11	18	14	16·0
(iii) *Paxillus involutus* strain 16	12	16	16	16·0
B. 55 weeks after transplanting				
Uninoculated control	79	31	Nil	15·5
Inoculated with:				
(i) *Hebeloma sacchariolens* strain 4	119	65	48	56·5
(ii) *Paxillus involutus* strain 3	68	39	44	41·5
(iii) *Paxillus involutus* strain 16	91	49	70	59·5

fungal species forming fruitbodies, the basis of the concept of 'early' and 'late' stage fungi, the former seeming to be more likely to sustain the benefits of inoculation.

In his presidential address to the British Ecological Society, Harley (1971) suggested that the prolific development of fruitbodies by mycorrhizal fungi might, because of their dependence upon their hosts, minimise the benefits that might otherwise have been conferred. While our knowledge of host dependency has recently been augmented by the abrupt cessation of fruitbody production when trees are defoliated (naturally or experimentally) (Last *et al.* 1979), much still remains to be learnt about mineral uptake by mycorrhizal fungi (Table 22). Does their prolific production of phosphatase enable them to extract tightly-bound organic forms of 'phosphate' from soil organic matter more easily than non-mycorrhizal litter decomposers such as *Mycena galopus* and *Marasmius androsaceus* (horse-hair fungus)?

F. T. Last, P. A. Mason, Julia Wilson and J. Dighton

Table 22. Estimates of acid phosphatase produced by isolates of mycorrhizal (M) and non-mycorrhizal (NM) fungi growing in Hagem's solution with 10 ppm P.

	Phosphatase produced, estimated as µg Phenol g^{-1} (dry weight of hyphae)
Lactarius rufus (M)	26,000
Paxillus involutus, isolate A(M)	15,000
Hebeloma crustuliniforme (M)	11,000
Paxillus involutus, isolate B(M)	8,300
Amanita muscaria (M)	5,700
Suillus luteus (M)	4,500
Mycena galopus (NM)	4,300
Marasmius androsaceus (NM)	710

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REPORT OF A SYMPOSIUM TO HONOUR CHARLES DARWIN, FATHER OF SOIL ZOOLOGY

Charles Darwin's interest in the activities of earthworms was triggered by his Uncle Josiah Wedgewood during the 1830s when Darwin was on vacation in Staffordshire. Wedgewood's observations, on the burial of marl on his estate by earthworm casting, led Darwin to develop this interest through to the publication of 'The formation of vegetable mould through the action of worms' in 1881. This book was received with 'almost

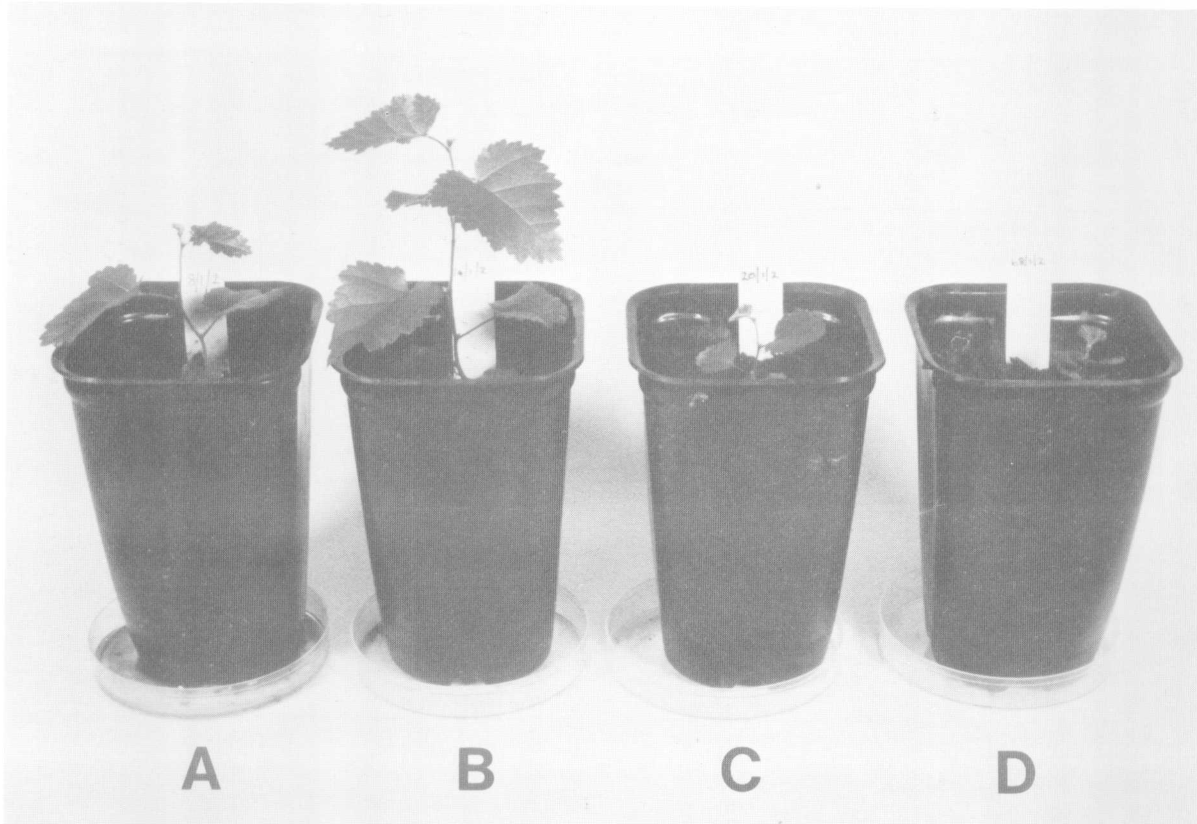
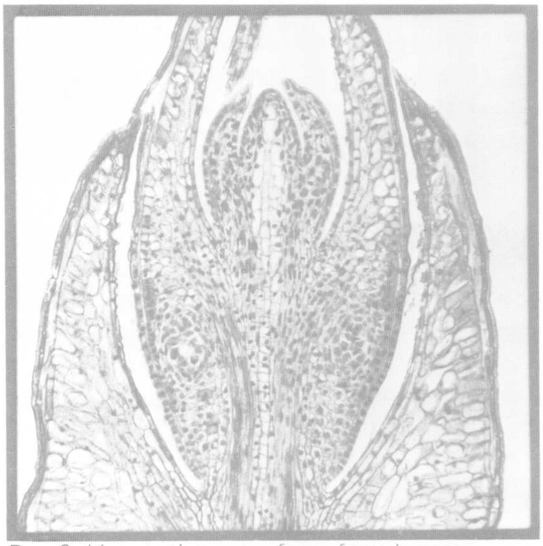


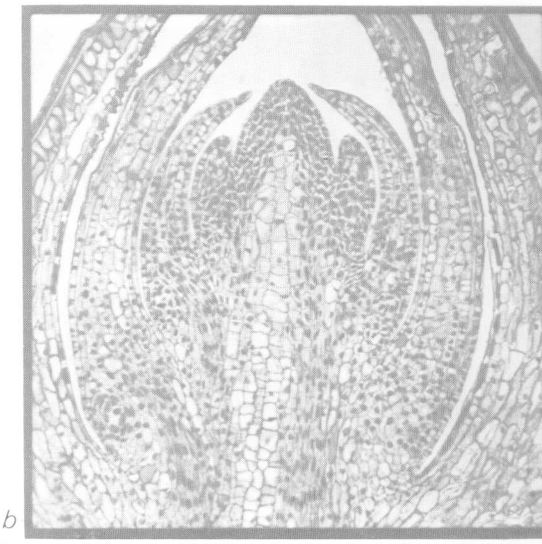
Plate 1—Growth in coal spoil (pH 3·9) of Betula pendula *seedlings inoculated during propagation with A, isolate 16; B, isolate 17; C, isolate 25 of the sheathing mycorrhizal fungus* Paxillus involutus *(brown rim roll); and D, propagated as for A, B and C, but without the addition of mycorrhizal fungi. Photographed 9 weeks after transplanting.*
Photograph P. A. Mason.

Plate 2—Contrasting clones of Picea sitchensis; *preliminary trials indicate that 5-year heights could be increased by 50—70% above Queen Charlotte Islands provenance by selecting the best 5% of clones.*
Photograph M. G. R. Cannell.



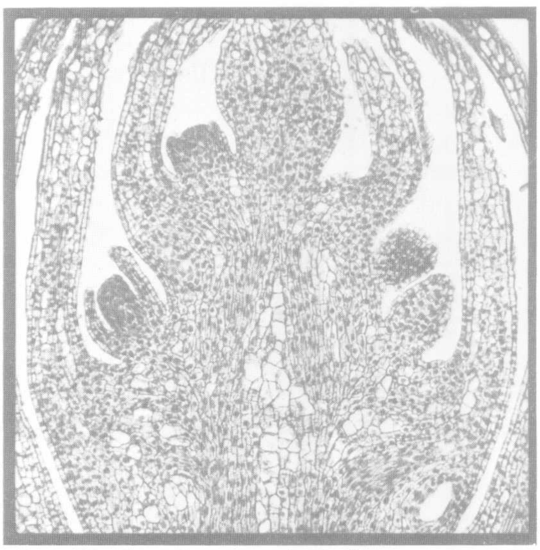
a

Day 0. Vegetative apex from female zone.



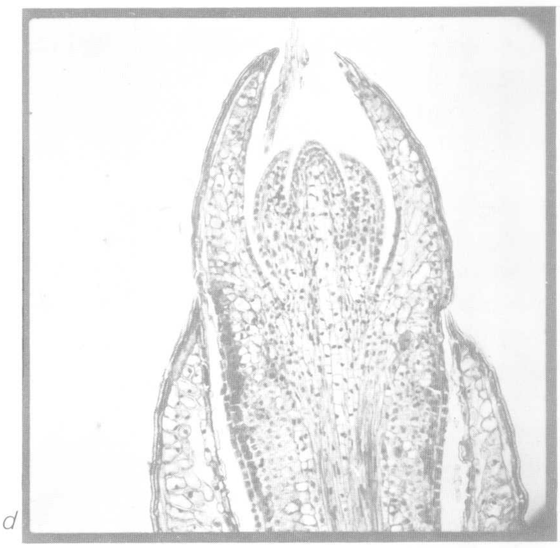
b

Day 28. Female apex, showing reduced internode elongation and early stages of formation of a cone scale.



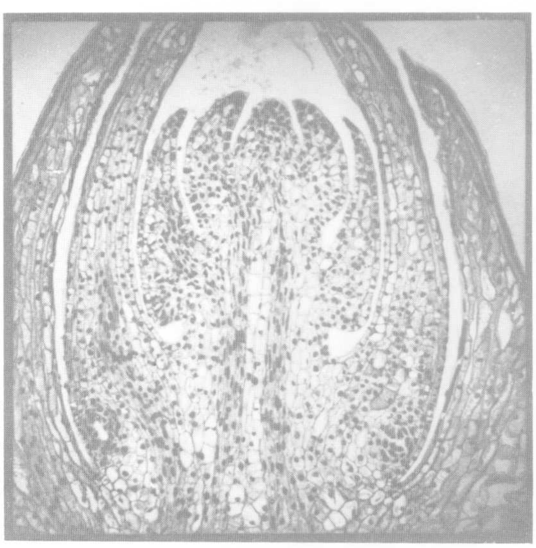
c

Day 56. Female cone, including on the left an ovule with its integument and micropyle.



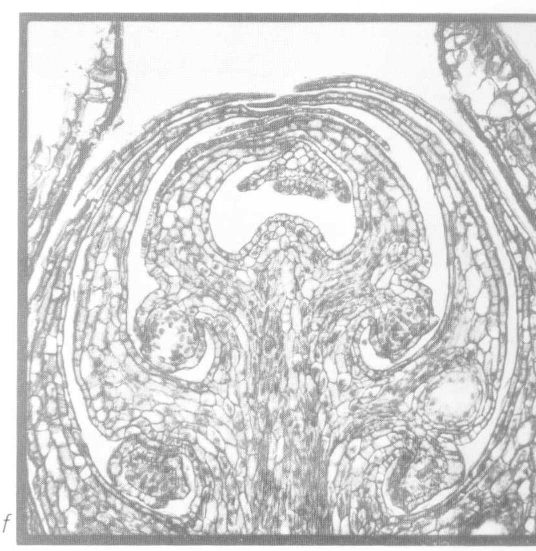
d

Day 0. Vegetative apex from male zone.



e

Day 28. Male apex, showing reduced internode elongation and early stages of formation of a cone scale.



f

Day 56. Male cone, showing some of the pollen sacs.

Plate 3 — Radial longitudinal sections through shoot apices from potted plants of Thuja plicata *clone 139, treated with 50 µg of gibberellic acid (GA_3) and kept under long-days in a heated glasshouse.*
Photographs K. A. Longman.

laughable enthusiasm' and, at one book fair, its sales were 4 times greater than the combined sales of 'The origin of species' and 'The descent of man'. To gardeners and farmers, and to the lay public, it provided a new view of earthworms: instead of being pests to be eradicated, as was currently considered, they were to be conserved as they help maintain soil fertility. From that time, Darwin has been considered as the father of soil zoology, possibly even of soil biology, and, because of the importance of the occasion, the centenary of the publication of 'The formation of vegetable mould', 140 scientists from 30 countries met at Grange-over-Sands, Cumbria, in August 1981, to honour Darwin and to review current knowledge of earthworms. The contributions to the symposium, organised by Dr J. E. Satchell, showed that Darwin's concepts, amplified and couched in modern chemical and physical terms, are still the cornerstones of soil ecology. But, notwithstanding, many new aspects and applications have been developed, some of which, particularly those relevant to terrestrial ecology in Britain, are discussed here. Papers from the symposium will be published by Satchell (in press) and in *Pedobiologia.*

Earthworms and soil properties

In summarising the theories underlying humus formation, a subject of considerable research, M. H. B. Hayes emphasised the role of polysaccharides found in earthworm mucus in the formation of aggregates and the stabilization of soil. Additionally, by bringing together inorganic and organic colloids, worms may greatly influence water and nutrient retention. However, the exact mechanisms for binding water and nutrients to soil inorganic particles and facilitating the stabilization of aggregates are still unclear. It is thought that bridges formed between inorganic and organic colloids by polyvalent cations are important.

Although Charles Darwin and his contemporary Gilbert White described the effects of earthworms on soil physical structure, little is known about the quantitative aspects of these effects. However, this deficiency is now being corrected. Thus, the distributions of stable isotopes of carbon (^{12}C and ^{13}C) and the radioisotope (^{4}C) are being used by J. D. Stout and others to estimate rates of organic matter turnover by earthworms. N. Martin, also in New Zealand, showed that growth rates of *Allolobophora caliginosa* and *Lumbricus rubellus*, 2 worms common in Britain, were directly related to amounts of soil organic matter consumed, the rate of soil consumption increasing as the soil organic matter content decreases. It seems that abilities to consume and assimilate soil explain the distributions of many species of worms. The extent of the movement of soil from one soil horizon to another is also dependent upon the species of worm and the physico-chemical environments. Evidence about soil movement is coming from analyses of concentrations of complexed organic matter and clays in the gut contents and casts of worms, comparisons being made with concentrations found in soil profiles (A. Kretzschmar).

The role of earthworms in the circulation of plant nutrients was emphasised in several papers. Although some gross quantitative estimates were produced for selected ecosystems, few resources are being allocated to the study of mechanisms controlling nutrient mobilization. J. K. Syers and J. A. Springett, in an analysis of temperate, managed grassland soils, showed that casts of *Allolobophora caliginosa* contain enhanced amounts of some plant nutrients when compared with concentrations in mineral soil that has not been consumed. In contrast, amounts of nutrients in casts of worms in litter and dung are rarely enhanced, but the proportions of plant-available nutrients are usually greater. This increase in the proportions of available forms is particularly noticeable soon after deposition, amounts of available phosphorus being shown, by using isotope labelling, to decrease thereafter. The studies of S. Matsumoto indicate that worm casts rich in sugars and amino acids support, in the short term, enhanced rates of microbial activity and mobilization of plant nutrients.

Grassland ecology

The populations and activities of earthworms in grasslands were analysed in a number of papers, with 2 being of particular interest. The natural colonization of the polders of the Netherlands by earthworms is slow: the absence of worms in an intensively used pasture in a reclaimed polder was associated with unproductive swards, weed colonization, soil impaction and accumulations of surface organic layers (M. Hoogerkamp, H. Rogaar & H. Eijsackers). However, 2 years after introducing *Allolobophora caliginosa* and *Lumbricus terrestris*, with dispersal rates of 9 and 4·5 m per year respectively, many of these undesirable aspects were lessened, with yields concomitantly increasing by 7–20%, part at least of the improvement being attributed to changes in soil physical structure, notably improved aeration. Infra-red and false colour aerial photography, supported by field measurements, showed that pastures with earthworms were warmer at night and cooler during the day than pastures without earthworms.

Darwin suggested that worms play an important role in the burial of plant seeds. During the symposium, J. Grant provided evidence to support this contention. Despite the small size of grass seeds, the larger species of worms were shown to ingest selectively seeds of different genera. Most of the ingested seeds were subsequently expelled (75-95%) and, although percentage germination was not decreased, rates of germination were slowed by 24–48 hours. Interestingly, 70% of the dicotyledon seedlings emerging from seed buried in a grassland emerged from those parts, 25% of the total area, covered by worm casts, the 'effects' of *Allolobophora longa* casts being 2–3 times larger than those of *Lumbricus terrestris.*

Earthworms in cultivated and reclaimed soils

Cultivated soils tend to support smaller populations of earthworms than grasslands or woodlands. In cultivated soils, the addition of organic manures and/or the retention of crop residues can be important if earthworm populations are to be sustained (C. A. Edwards; A. Lofs-Holmin; C. Anderson). Modern methods of direct drilling, like the application of pesticides and fertilizers (excepting ammonium), foster the development of earthworm populations which are adversely affected by intensive cultivations. The latter, often associated with depletion of soil organic matter, can decrease numbers and species diversity, the repeated destruction of habitats particularly affecting deep-burrowing species.

Agricultural experience is relevant to the reclamation of industrial wastes and *vice versa*. Thus, the effects of disturbance and organic matter were found, when studying mine wastes (V. Standen & G. B. Stead; J. P. Vimmerstedt) and reclaimed cut-over peat (J. P. Curry & D. C. F. Cotton), to parallel closely those described on good mineral soils. Stored top soil may contain large numbers of worms, but these may be lost when the soil is redistributed. Although attention is paid to the appropriate selection of plants and mixtures of fertilizers when reclaiming derelict sites, little or no concern is shown towards the establishment of conditions favouring earthworms, despite their importance and the availability of successful methods for introducing worms.

Transfer of heavy metals

Interest in the role of earthworms in the mobilization of pollutants has been focused on heavy metals. Earthworms accumulate cadmium, zinc, lead and copper in a variety of conditions, the actual amounts depending on interactions between the different heavy metals and between the heavy metals and other elements, particularly calcium. It was shown that these accumulations can be transferred to decomposers in more labile forms on death or can be passed from worms to their predators (M. Ireland; A. Carter; Wei-Chun Ma).

Vermiculture

It is unlikely that Darwin envisaged the collection and intensive cultivation of earthworms for protein or their potential usefulness in waste disposal. *Eisenia foetida* and *Perionyx excavatus* have been successfully and intensively cultivated for fish food on a variety of organic wastes, it being suggested that their large protein content, up to 70% in the case of *P. excavatus*, makes them 'highly acceptable as human food' (R. D. Guerro; Kale *et al.*). By using simple and efficient means of harvesting, crops of *Lumbricus terrestris* valued at £6 million are annually exported from golf courses and pastures in Ontario, Canada (A. D. Tomlin).

The quality, including the physical condition, of organic substrates is critically important for worm cultivation. Current research, including that in ITE, tends to concentrate on *E. foetida*, with its capability of utilizing combined wastes ranging from liquid animal slurries from agriculture to solid urban wastes (A. Kretzschmar; L. Fayolle; E. F. Neuhauser & M. R. Malecki). With the utilization of wastes, and therefore decreased net costs of disposal, the provision of a useful protein crop and the bonus of humus of commercial value, the cultivation of worms seems to have economic potential. The provision of humus is a reminder of Darwinian ideals, as is the idea that the variety of earthworms, lumbricids, includes a wealth of diversity from which to select species for particular purposes (Satchell 1980).

In summary, the symposium brought together a wide variety of interests and expertise to focus on the ecology of an animal whose importance is often greatly underestimated. It stressed, in no uncertain manner, that their management, whether in agriculture, derelict land reclamation or vermiculture, necessitates a detailed understanding of physiology, behaviour and performance, and the response of these to the environment. Earthworms are essential components of many terrestrial ecosystems, but their control by competition and predation, aspects of classical population control theory, appears to be of marginal relevance. The success of earthworm communities seems strongly dependent upon partitioning between species of organic matter in different phases of decomposition. Earthworm ecology is now making a major contribution to the wider sphere of population ecology.

O. W. Heal

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Research of the Institute in 1981

Introduction
As in previous years, the main section of the Report describes some of the research projects being undertaken within the Institute, while the full list of project titles is given in Section IV. These relatively short accounts have been grouped according to the Subdivision of the Project Leader, within the 3 Divisions of the Institute.

Within the Animal Ecology Division, 5 short accounts describe some of the work of the Subdivision of Invertebrate Ecology, followed by 4 reports of research within the Subdivision of Vertebrate Ecology, and 9 contributions from members of the Subdivision of Animal Function. Within the Plant Ecology Division, 7 reports describe some of the work of the Subdivision of Plant Biology, followed by 8 contributions from the Subdivision of Plant Community Ecology, and 5 accounts of work from the Subdivision of Soil Science. The 3 Subdivisions of the Scientific Services Division – Data and Information, Chemistry and Instrumentation, and the Culture Centre of Algae and Protozoa – each present their reports in 2 parts. The first part gives a general review of their service functions during 1981, while the second part describes some of the research projects being done by members of the Subdivision.

Invertebrate Ecology

THE RATE OF INFILL AND COLONIZATION BY INVERTEBRATES OF BORROW PITS IN THE WASH (SOUTH-EAST ENGLAND)

(This work was largely supported by Central Water Planning Unit (DoE) funds)

As part of a study into the feasibility of building a freshwater reservoir in the Wash (Anon 1976), 2 engineering trial banks were constructed on Breast Sand, an area of mud and sand flats bounded by the Rivers Nene and Great Ouse. These banks were used to test the suitability of local sediments as building material for the impounding walls. From studies carried out on the first trial bank, built on the higher mud flats in 1972, it was realised that only part of the material required to construct the impounding walls of a reservoir could be obtained from within the designated area. The remainder would have to be obtained from outside the area, and the borrow pits thus created would be an additional, though temporary, loss of wader and wildfowl feeding areas. Some indication of the likely recovery time of these areas was required. Accordingly, the rate of infill of the borrow pit of the outer trial bank, constructed in 1975, in the *Arenicola* sand flats, and the rate of colonization by suitable food organisms for birds have been studied. The borrow pit of the inner trial bank was also sampled, 3–4 years after its excavation, when it was in an advanced stage of infill and had an abundant fauna.

The outer borrow pit had a volume of 458 000 m^3 when excavated, but, after one year, was already 44% infilled. However, at this time, the water in the pit began to drain down sufficiently at low water to allow the development of a waterfall along the northern (downshore) edge of the pit, as the flood tide advanced. This waterfall prevented further deposition of sediment in the northern half of the pit until, after 6 months, a lagoon (22 500 m^3) was eroded from the north-west corner, which allowed the pit to fill with water in advance of the flood tide. The pit was 99% infilled after 3·5 years. The changing volume of the pit was adequately described by a linear regression equation: $Y = 3393\text{-}114\ X$ ($r^2 = 0{\cdot}94$), where Y = volume of pit in $m^3 \times 10^3$ and X = time from excavation in years. The rate of sedimentation in the outer borrow pit, though decreasing with time, was considerably greater than previously recorded rates for intertidal banks, and probably accounted for the paucity of fauna in the pit until completely infilled. Though excavated in an area of fine-medium grained sands, unconsolidated, anaerobic, clay and silt sediments initially accumulated in the outer borrow pit with up to 5 cm of liquid mud at the surface, but, after 2 years, the predominant fraction was fine sand. Even then, when the water drained completely at low water, the surface sand was extensively cracked and was soon buried by mud bubbling up from below, a phenomenon created by escaping natural gas. Indeed, it was only after complete infill that a stable surface of >5 cm fine sand was established. In contrast, the inner borrow pit, which was excavated in an area of clay and silt sediments, infilled with coarser, sandy sediments.

Only *Nepthys hombergii* became established in the outer borrow pit before it was completely infilled, when the other pre-excavation dominant species returned. Other, mainly bivalve mollusc, species were found in low densities, but these were all washed into the pit from the adjacent sand flats and survived for only a short period before being buried too deeply by the rapidly accreting sediments. In the absence of other species in the borrow pit, *N. hombergii* attained greater densities than found in the area before excavation. *Capitella capitata* and oligochaete species (opportunistic, 'pollution indicator' species) were not the first colonizers, as expected, and the oligochaete *Peloscolex bendenii* was the most abundant species in the inner borrow pit when completely infilled 4 years after its excavation. The density of invertebrates in the borrow pits was greater than in the surrounding mud flats, and was a focus for birds feeding in the area. The outer borrow pit, after complete infill, also had higher densities of bird food species than before excavation, but was rarely visited by birds.

S. McGrorty and C. J. Reading

Reference
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HABITAT PREFERENCES OF SPIDERS ON HEATHLAND

Our knowledge of the detailed habitat preferences of even the more common spiders is generally rather poor, and is often limited to what is little more than a catalogue of chance captures, with little indication of the real habitat preference. In this study, a quantitative approach has been applied to the habitat preferences of 45 spider species occurring on an area of typical Dorset heathland. The 8 ha site on Hartland Moor National Nature Reserve (NNR) contained most of the major heathland vegetation types found in Dorset, whilst a good range of altitude further increased the diversity.

Twelve habitat variables were measured at each of 154 random sample points, and a single pitfall trap was used at each point for one year. The habitat variables measured were altitude, soil moisture, integrated temperature in July, maximum height of the dominant ericaceous plant, and percentage cover of the 7 major plant species, plus bare ground. The weighted means of each of the 12 habitat variables were calculated for each spider species, and a correlation matrix produced. Principal component analysis was then applied, and 4 uncorrelated components were extracted accounting for 85·38% of the habitat variation.

Component I (30·6% of total variation) represented the variation from a cold, heavily vegetated habitat, with mat/tussock-forming plants between tall bushes of *Erica cinerea*, to a warm, open habitat with areas of bare ground and *Calluna vulgaris* or *Erica tetralix*. Component II (27·1%) represented, at one extreme, high, dry *C. vulgaris* or *E. cinerea*, and, at the other, low-lying wet *E. tetralix* and *Molinea caerulea*. Component III (20·4%) was the variation from the high, dry *E. cinerea/Agrostis setacea* zone to a lower-lying habitat dominated by *C. vulgaris*. Component IV (7·4%) represented areas of *Pteridium aquilinum* in warm, open situations.

The individual scores were calculated for each spider species on each component, allowing the relative position of each species to be plotted in a hypothetical habitat hyperspace. As shown in Figures 20 and 21, most of the spider fauna studied was scattered throughout the more moderate habitats of the heath. However, 9 species showed preferences for more extreme conditions. *Gnaphosa leporina* (4) had a strong preference for low, wet areas of *Sphagnum* carpet. *Pardosa pullata* (11) showed a stronger affinity for low, wet heath than other species, but preferred longer vegetation than *G. leporina*. Both *Xysticus erraticus* (9) and *Alopecosa accentuata* (13) showed a very strong preference for the high, dry *E. cinerea*/A. *setacea* zone.

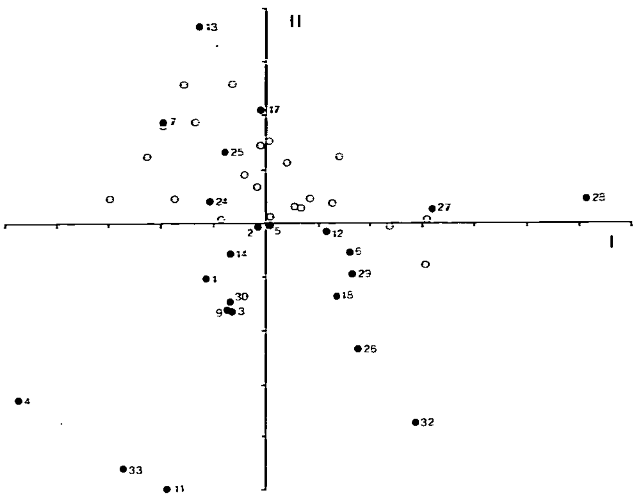

Figure 20 Position of spiders in component space (Components I and II).

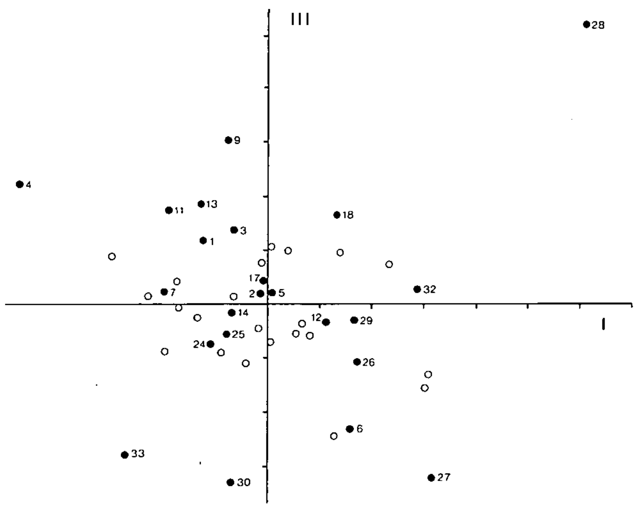

Figure 21 Position of spiders in component space (Components I and III).

Walckenaera unicornis (27) seemed to prefer long, dense *C. vulgaris* at a moderate height, whereas its congener, *W. cuspidata* (28), with the most extreme habitat preference of all the 45 species, was found in the coolest, most heavily vegetated areas of *E. cinerea*, with *A. setacea* or other mat-forming plants. *Pocadicnemis pumila* (32) and *Hypselistes jacksoni* (33) were both associated with low, wet areas, but the former prefers less dense vegetation. *Maso sundevalli* (30) was rather similar to *W. unicornis* in habitat preference, but, here again, it seemed to prefer rather less dense vegetation.

This approach to the problem of habitat preference in spiders has shown some interesting differences between closely related species which may help to explain methods of resource partitioning and co-existence.

R. G. Snazell

RECOLONIZATION OF HARTLAND MOOR BY SPIDERS

A fire on Hartland Moor NNR, Dorset, on 14–16 August 1976, which covered an area of about 200 ha and completely destroyed about 80% of the area of dry heathland on the reserve, provided an opportunity for a major study of the recolonization of the burnt area by spiders. The important features of this fire were that its intensity and the area it covered were greater than in previous studies, and a large part of the burnt area was surrounded by farmland used for grazing cattle and horses, so that there was no adjacent heathland from which spiders could migrate. As most species of spiders can migrate aerially, this lack of adjacent heathland might not have had any serious long-term effect, but the recolonization rates of burnt areas close to unburnt heathland, and close to farmland, were thought worth comparing. Previous work on smaller burnt areas had shown that spider populations and species composition change rapidly during the first 5 years after burning, the rate of change then slowing down between 5–10 years, but still continuing for at least 20 years after burning.

Changes have been studied on 8 plots in the burnt area, 2 being close to adjacent farmland, 2 close to unburnt heathland, 2 in the centre of the burnt area, and 2 in wet heath, which was burnt less severely than the dry heath. During the first 3 years (1976–79), 9 pitfall traps were used continuously to collect ground-active spiders, and 6 water traps supported about 10 cm above ground level were used to catch aerial immigrants. After 3 years, the number of pitfalls at each plot was reduced to 6, and the water traps were reduced to 4 on the dry heath plots and removed altogether from the 2 wet heath plots. In addition, as a comparison, 8 0·25 m^2 quadrats on each plot were searched by hand for spiders on 3 occasions in 1979, and 10 1 m^2 samples were taken on each plot with a D-vac suction net on 3 occasions in 1979 and 1980. The vegetation cover was recorded and photographed on one fixed quadrat near each pitfall and water trap in April 1978, September 1979 and July 1981. The results from the pitfall and water traps have been summed to give total numbers for each type of trap per year in each plot. Altogether in the first 5 years, 246 species were trapped, 186 in the pitfalls and 191 in the water traps. The results have proved to be of interest in 3 main ways. First, the rate of recolonization by spiders has generally been slower than in areas studied previously, probably because of the size and severity of the fire and the presence of unburnt heathland only at one end of the burnt area. For example, the linyphiid *Phaulothrix hardyi*, which in previous studies reached maximum numbers in the second year after burning, is still increasing after 5 years, and the theridiid *Steatoda albomaculata*, which previously reached its peak in the first year, attained maximum numbers in the third year after burning in this study. Second, there have been striking differences between the spiders caught in the pitfalls and those taken in the water traps. The latter have caught several species which are never normally found on heathland, and others which, although occurring on heathland, would not normally be found in the type of habitat where the traps are situated; for example, several species of theridiids which spin webs on large gorse bushes have frequently been caught in areas well away from such bushes. These species have been trapped during random aerial dispersal; they would not have stayed in the habitat where they alighted, and have therefore not been caught in the pitfalls. Conversely, the spiders caught in the pitfalls have nearly all been typical heathland species, and some species of gnaphosids, common in the pitfalls, have not been taken in the water traps, either as adults or juveniles. Third, it was observed that some of the species typical of recently burnt heathland (eg *Phaulothrix hardyi*) appeared first on the plots nearest to the unburnt heath, spreading to the other plots and increasing in numbers during the second and third years; also, some species typical of grassland (eg *Oedothorax apicatus*) appeared on the plots nearest to the grassland in the first 2 years, but gradually disappeared thereafter.

The water traps have now been removed, because aerial immigration has ceased to be an important factor, but pitfall trapping will continue, possibly on a reduced scale, for at least a further 5 years.

P. Merrett

THE ROLE OF YOUNG WORKERS IN THE DEVELOPMENT OF AN ANT SOCIETY

Ant societies grow from small groups of workers and queens by adding more workers than they lose from death; as they grow, their composition changes, which means that the ratio of workers:queens increases and the age structure becomes biased towards the young. A thorough study of the effect of the worker:queen ratio has been completed (Brian *et al.* 1981), and research is now focused on the role of young workers in population development, to determine what part young workers play in triggering sexual production and a re-entry of inseminated queens. When new queens are added, workers are not, as both come from the same type of uncommitted labile female larvae; hence, the worker:queen ratio drops. The colony reproduces by fission and the emigration of worker:queen buds initiates another cycle.

The essential control over male production comes from the queens, which can influence worker egg formation, stopping males even being initiated and diverting nutriment to female larvae derived from eggs laid by the queen. In the species used for experimental work (*Myrmica rubra*), males arise from worker eggs which remain unfertilized and are able to develop parthenogenetically. To exercise this control, the queen either has to be laying herself, or to have produced a fresh egg mass. Smeeton (1981; NERC student at Furzebrook, 1975–78) found that, unless workers experienced this queen control at, or soon after, 'birth', ie when they emerged from their pupal skin, they laid male-giving reproductive eggs. Thus, their egg production system is working as if there were no queen in the society; the young adult, whilst still in the pupal skin, may well be developing oocytes and, not surprisingly, cannot be influenced by queen behaviour. It could, however, be affected by a volatile pheromone, although none is known to exist. From Smeeton's work, it appears that, from the age of 3 weeks, workers can lay male eggs for 2 weeks, even in the presence of egg-laying queens. This, then, is an important point: workers at birth are reproductive and male-biased; they have to be converted to secreting food (laying trophic eggs) for female larvae. The queens have to 'make' them rear female larvae.

Although queens can do this in the autumn, they cannot 'make' workers bring larvae into a state for metamorphosis, which is partly governed by daylength and inbuilt diapause stages in larvae, but partly, we think, by whether workers regurgitate enough digested juices to affect larval development. However, at that season, it is appropriate that metamorphosis cannot be stimulated, since the third instar larva is the only brood stage that can hibernate successfully. By their inability, or failure, to respond to queen 'pushing', workers steer the society on to a hibernation course in autumn.

When spring comes, all is then clear for metamorphosis, but queens must guard against workers forming sexuals out of female larvae. Queens are able to stop them over-feeding caste-labile female larvae, as well as being able to stimulate them to feed worker-biased female larvae, but this can only be done at close quarters, virtually in the same chamber. This brood-feeding effect on workers is quite different from the egg-laying effect; for one thing, a dead queen can do it, as it is caused by a low volatility contact pheromone in the skin. It has been shown that, in spring, younger workers are liable to ignore the instructions of the queens, and, in societies with a high proportion of young workers, caste-labile larvae are fed copiously to produce sexual females (Brian & Jones 1980).

The question can, therefore, be asked: why are young workers sometimes refractory to queens? For a clue, we referred to Carr (1962) who produced evidence that early experience in larval or early adult stages of queens caused stronger reaction later on. A specially designed experiment by E. J. M. Evesham (another NERC student, 1979–82) confirmed Carr's evidence, and added the point that the young adult has a sensitive phase which influences its reaction to queens in later life. This reaction is compounded of the ability to suppress female larvae with a queen nearby, but to foster the same larvae if there is no queen, or if she is merely encountered occasionally. Both reactions, positive and negative, are increased by the early experience of a queen, which indicates that the refractory attitude of young workers even in spring, and their unresponsiveness to queens that causes them to nourish caste-labile larvae, may well be caused by an inadequate queen education in early life, perhaps as a direct result of the high worker:queen ratio in 'mature' societies. Further work is continuing on this intriguing system of education in ant societies.

M. V. Brian and E. J. M. Evesham

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RELATEDNESS BETWEEN QUEENS AND WORKERS IN THE MULTI-QUEENED COLONIES OF *MYRMICA RUBRA*

Relatedness between queens in multi-queened social insect colonies is of interest because high levels of relatedness may explain co-operation between these queens. Hamilton (1964) formulated the relationship $K > 1$ as a minimum condition for co-operation, where K is the ratio of the gain by the beneficiary to the loss of the altruist, in terms of offspring produced. By introducing relatedness (r) between beneficiary and altruist, the minimum condition for co-operation becomes $K > 1/r$. If r is high, co-operation is explained. Since r can be measured more easily than K, estimates of r have been used when seeking an explanation for such co-operative behaviour. Orlove (1975), Craig and Crozier (1979), and Pamilo and Varvio-Aho (1979) have developed and used a regression method for estimating r, thus circumventing the need for pedigree information, which is often unobtainable. The regression method estimates b as the regression coefficient of the frequency of an allele in each individual in a nest, plotted against the mean frequency of that allele for the whole nest. When there is no selection, b = r. This technique was applied to the multi-queened ant species *Myrmica rubra* by Pearson (1982), using a 2-allele esterase polymorphism, and the relatedness between the colony queens was assessed. Similar estimates have been made of worker relatedness in these colonies. Two colony populations of *M. rubra*, separated by a distance of several kilometres, were examined over a 2-year period. The regression coefficient b for intra-colonial relatedness of queens was found to be without statistical significance, except for one population in one year, which suggests that a high level of relatedness is not a pre-requisite for co-operation in this species. The one significantly high value for r may have been a consequence of sampling which temporarily raised intra-colony recruitment of replacement queens.

This explanation raises problems in distinguishing between high r values as a cause of co-operation and high r values caused by, say, an ephemeral habitat where queen mortality is high, thus raising intra-nest recruitment of queens. This distinction is significant in the context of Holldobler and Wilson's (1977) suggestion that ephemeral habitats may provide an ecological reason for co-operation in multi-queened colonies — an explanation which provides an alternative, if r for colony queens is low.

Similarly, workers in these colonies were found to be not significantly related, except in one instance, which indicates that queens do not parasitise each other, and that there is no 'dominance hierarchy', in the sense that all the queens produce workers. It may, in fact, be difficult for the queens to parasitise each other by not producing workers, ie not contributing to colony costs, but reaping the benefits, because the workers are instrumental in caste determination (Brian 1967). On this analysis, it may be that the workers control caste determination, or even that this control evolved as a safeguard against the unstable state of intra-colony parasitism, which leads to extinction, or single-queen colonies.

Lack of worker relatedness raises other problems for the colony. A conflict of interest may be expected between queens and workers over queen recruitment, as this lowers worker relatedness and reduces the possibility of workers maximising their inclusive fitness through sex ratio manipulation (Trivers & Hare 1976). If this is so, it has to be assumed that recruitment of queens in some way benefits the existing colony queens, as, without this assumption, it is difficult to see why recruitment — and hence multi-queened societies — would occur in *M. rubra.* How true this assumption is can only be guessed at present. The problem is: why should established queens permit unrelated queens to share their investment? One answer is that there may be a mutual advantage accruing to both parties. When colonies are founded, even in species where one queen per colony is the norm, they are founded by a group of queens. Once a colony is established in a uni-queen species, one queen takes over. The need for many foundresses may derive from the necessity to produce workers rapidly, for such reasons as defence of a foraging area of sufficient size for the colony to survive and grow, and eventually reproduce. If a habitat is unstable with reference to the species' requirement, colonies may be subjected to repeated catastrophes, reducing the colony at frequent intervals to 'foundation conditions', ie the colony may spend much of its time in the colonizing phase, so requiring a permanent number of queens. If this explains queen co-operation in *M. rubra*, it is testable where suitable habitat parameters can be isolated. Variation in all or one of these parameters may relate to queen number or, conversely, lack of variation should tend towards the development of single-queened colonies.

B. Pearson

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Vertebrate Ecology

FAECAL PELLETS AS INDICATORS OF BODY SIZE IN RED DEER

Mammals, even quite large ones like deer, can be very difficult to study by direct observation in their natural habitats (Plate 6), and modern methods of indirect observation, such as radio tracking or the use of automatic recording equipment, may be precluded by difficulties of catching the animals or by the cost of equipment. Often, therefore, the only feasible approach is to try to interpret the tracks, signs and waste products left by the animals, as these are usually more visible and accessible than the animals themselves.

The value of indirect information on the presence and whereabouts of animals has long been appreciated by hunters and naturalists (Bang & Dahlstrom 1974), but the problem for ecological investigators is to provide scientific justification for the ways in which such clues can be interpreted, eg in terms of species present, their levels of abundance, patterns of dispersion, group

Plate 4—Demographic studies on seedlings at Clipsham quarry. Coloured rings mark seedlings of Gentianella amerella.
Photograph D. G. Park.

Plate 5—Radio tagging a grey squirrel to study behaviour in damage-prone woodland.
Photograph R. E. Kenward.

Plate 6 — Red deer are often difficult to study by direct observation in woodland habitats. Hind in Fiunary forest. Photograph B. Mitchell.

Plate 7 — With red combs raised, a captive red grouse cock threatens the photographer R. Moss.

composition, etc. Jenkins and Harper (1981), for example, used the appearance of very small otter footprints as a means of detecting when breeding had occurred. Some ecologists have also tried to census small groups or populations by counting individually recognisable footprints; given a small enough number of animals, and a suitable substrate, the assumption is that individuals can be identified (and tallied) from the measurements, or other natural peculiarities, of their prints. However, the limitations of the latter approach are quite obvious. Much more attention has been given to the use of faecal depositions as indicators of population density and site use, especially with large mammalian herbivores. This is one of the methods being tested in current ITE research on the assessment of red deer populations in commercial forests in Scotland (Mitchell & McCowan 1980). This research also prompted questions on other useful inferences which might be possible from studies on faecal depositions, eg can sex and body size be predicted from measurements of faecal pellets?

In deer, as in other polygynous mammals, adult males are, on average, appreciably larger than adult females, but with some overlap, and it would be reasonable to expect similar differences in other (non sex-specific) anatomical features which change with body size. Therefore, body size, or some index of body size, would only be a rough guide to sex. In fact, this difficulty was shown for hoof size (and hence track size) of North American black-tailed deer (McCullough 1965), in a study to determine whether these animals could be sexed reliably from their hoof tracks. Our interests were centred on 2 possible uses of faecal pellet measurements: (i) to decide whether specific sites are used mainly by stags, or by hinds and their dependants; and (ii) as a means of comparing the size distributions (and, possibly, the levels of performance) between red deer populations. Clearly, the key problems were to determine if faecal pellet size does reasonably reflect body size, and if this relationship is constant between populations.

Data were collected in 3 contrasting areas, the aim being to obtain carcase weights, measurements of skeletal size, and samples of faecal pellets from a wide range of ages of both sexes of red deer. Samples of fresh pellets were collected in winter at Glensaugh experimental deer-farm, by following the tamest marked individuals until they defaecated. Recta, jaw bones and carcase weights were also collected from red deer shot on the Isle of Rhum and at Glenbranter Forest in the statutory shooting seasons: mainly August to early October for stags, and November to early February for hinds. Unfortunately, most of the stag recta contained only soft dung, presumably because of the time of year when they were shot; in some habitats, red deer produce amorphous dung in summer and pellet groups in winter. Another limitation was that the measurements of body size were not all comparable between areas; live weight and hind foot (metatarsus) length were measured at the deer-farm, eviscerated carcase weight (and dressed carcase weight for some individuals) and jaw bone length on Rhum, and dressed carcase weight and jaw bone length at Glenbranter.

Pellets were typically bullet-shaped (approximately cylindrical with one end flattened and the other pointed), with remarkably little variation in shape or size (volume, weight, length and width) within samples, but with very much greater variation between samples – especially in the ratio of length to width. Preliminary tests showed that pellets were easier to measure after air-drying to constant weight (24 hours at 80°C) than when fresh. Air-drying gave consistent amounts of shrinkage in volume and linear measurements with no apparent increase in variability. The moisture content of fresh pellets was 68–70%, but that of soft (summer) dung was higher and much more variable (75–90%).

Table 23 summarises the main results, expressed as correlations between each pair of variables, and arranged according to body size features, pellet size features, and relationships between pellet and body size. Carcase weight and skeletal size were highly correlated, as might be expected. Amongst pellet features, length showed the poorest relationships with the others, perhaps because pellet length was more variable between individual deer, as also indicated by field observations. Similarly, amongst the relationships between pellet size and body size, those based on pellet length were by far the poorest. However, it was difficult to decide which of the other pellet measurements offered the best predictions of body size, and, indeed, of which aspect of body size. Examining these relationships graphically (see Figure 22 as an example) showed that much of the unexplained variation ($1-r^2$) was caused by individual scatter and not by curvilinear relationships. In fact, data transformations (not shown here) only marginally improved some correlations.

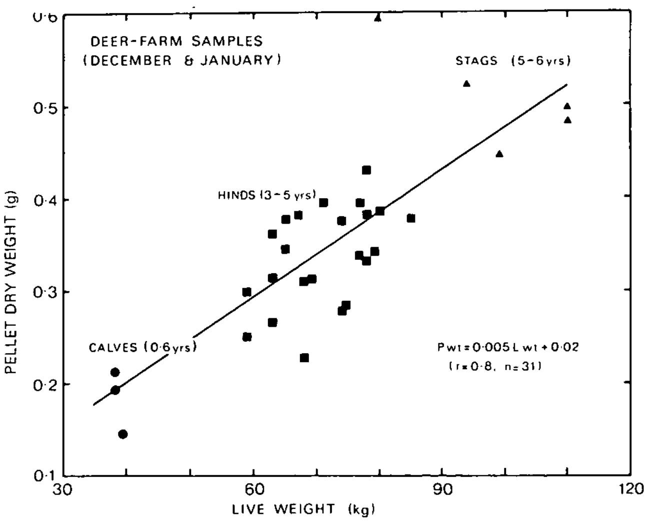

Figure 22 Deer-farm samples (December and January).

Table 23. Inter-correlations of body size and faecal pellet measurements in red deer, using data from live deer at Glensaugh experimental deer-farm and from deer shot on Rhum and at Glenbranter.
Values given are correlation coefficients (r's).

Source	Deer-farm	Rhum	Glenbranter
Number of deer	31	83	50
Classes	(stags, hinds and calves)	(hinds and calves only)	
a. Body size features			
Carcase weight/skeletal size	0·95	0·86	0·91
b. Pellet size features			
Dry weight/volume	0·93	0·85	0·91
Dry weight/length	0·53	0·49	0·82
Dry weight/width	0·92	0·77	0·82
Volume/length	0·59	0·39	0·66
Volume/width	0·91	0·70	0·76
Length/width	0·30	-0·001	0·53
c. Pellet size/animal tissue			
Pellet dry weight/carcase weight	0·80	0·63	0·56
Pellet volume/carcase weight	0·75	0·63	0·43
Pellet length/carcase weight	0·34	0·24	0·25
Pellet width/carcase weight	0·75	0·58	0·65
Pellet dry weight/skeletal size	0·79	0·68	0·50
Pellet volume/skeletal size	0·79	0·49	0·46
Pellet length/skeletal size	0·38	0·35	0·55
Pellet width/skeletal size	0·76	0·60	0·56

Notes:
1. Carcase weights used = live weight (deer-farm), eviscerated carcase (Rhum) and dressed carcase (Glenbranter)
2. Skeletal size measurements = hind foot length (deer-farm) and jaw bone length (Rhum and Glenbranter).
3. Pellet measurements made after drying to constant weight, using 10–15 pellets per sample.

Tests for consistency between areas in the relationships between pellet size and body size, using linear regression analysis, were possible only with the data from Rhum and Glenbranter, ie pellet volume, dry weight and width in relation to jaw bone length and dressed carcase weight. The detailed results are unnecessary as the relationships clearly differed between areas. In short, the deer on Rhum had significantly larger pellets than those at Glenbranter for a given carcase weight or jaw bone length.

The main conclusion is that faecal pellet size depends on other factors, probably diet, as well as body size. Even so, the existence of a reasonably strong association between pellet size and body size is still useful for making comparisons of range use within an area, but not for making indirect comparisons of body size between populations.

We thank the Rowett Research Institute and the Hill Farming Research Organisation for access to the deer at Glensaugh experimental deer-farm. We also thank Mr G. Sturton BEM (NCC deer stalker) and the Forestry Commission rangers for the material and data from Rhum and Glenbranter, respectively.

B. Mitchell and D. McCowan

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INHERENT CHANGES IN AGGRESSIVE BEHAVIOUR IN RELATION TO POPULATION REGULATION IN RED GROUSE

Two useful ideas have been circulating among students of population regulation in animals during recent years. First is the discovery that marked differences can occur in the frequency of many genes, both amongst adjacent animal populations and within the same population in different years or seasons. The second is that quite simple models of animal populations can cause oscillations in numbers, a fact that has led to the realisation that there is nothing magical about cyclic fluctuations in animal densities, and that an infinite series of cyclic causes is not necessary to explain cyclic phenomena. Combined, these ideas give rise to the hypothesis that the increase and decrease phases of cyclic population fluctuations are accompanied by different selective pressures. Hence, certain genotypes increase in frequency during one phase and decline during the other. This hypothesis has been thoroughly confirmed in microtine rodents. More speculative is the suggestion that cycles are actually caused by interactions between 2 genotypes, which, at its simplest, implies that aggressive individuals are at an advantage at high densities, but, when the frequency of aggressive genotypes becomes high, changes in spacing behaviour result in fighting, dispersal and population decline.

The first attempts to test this hypothesis were with microtines and relied on the identification of genetically determined blood proteins which changed in frequency with the phase of the cycle. The functions of these proteins were unknown, but it was hoped that they might, in some way, be linked to the behavioural processes which were thought to cause the fluctuations in numbers. Such a link was difficult to substantiate, and artificial selection for one such protein in wild populations failed to achieve any effect on population density (LeDuc & Krebs 1975).

Our approach with red grouse has been different (Plate 7). We first established that changes in dispersal, initiated by changes in spacing behaviour, did indeed cause changes in density (Watson & Moss 1980). Next, we studied inherent variations in aggressive behaviour in a population during the course of a fluctuation in numbers, by taking samples of eggs each year, hatching and rearing the chicks from these eggs in standard conditions in captivity, and then assessing aggressive behaviour once the chicks were fully grown. The main method was to keep the birds from one year to the next, and then compare successive year classes directly by putting birds from them together and assessing their 'dominance rank' (Figure 23), a rank similar to a conventional pecking order in chickens. By further work in the aviary, we then showed that the ability to dominate others was a heritable trait (heritability about 0·5), probably determined genetically as in chickens, although we could not prove this fact unequivocally, only that the trait was transmitted from parent to offspring. However, the transmission of traits from parents to offspring is all that is important from the point of view of explaining fluctuations in animal numbers — and, indeed, evolution. Marked differences in the mean dominance rank of a population could be achieved with only one or 2 generations of selection (Figure 23). The observed pattern of changes in the birds' inherent ability to dominate others is shown in relation to population density in Figure 24 (from Figure 1 in Moss & Watson 1980). This and other evidence suggest that natural selection against this trait was occurring during the increase phase of the fluctuation and for this trait during the decline. The latter suggestion agreed with the prediction of Chitty (1967), who was the first to propose the '2-genotype' model. However, changes in the inherent nature of the population are not shown to cause the observed fluctuation, merely to accompany it. Nonetheless, the work does confirm that selection for and against behavioural characteristics important for population regulation does occur on a short ecological timescale.

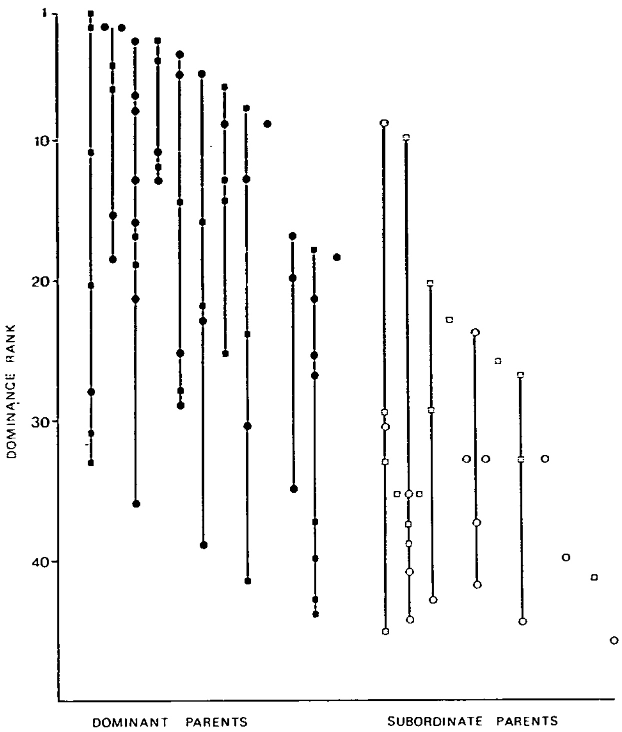

Figure 23 Dominance ranking of cocks (squares), and hens (circles), with selected dominant (solid) and subordinate (open) fathers and mothers in the second generation of selection.

R. Moss and A. Watson

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THE IMPORTANCE OF POLYGYNY TO HEN HARRIERS

The main aim of work on the Orkney population of hen harriers (*Circus cyaneus*) from 1975–1981 was to study the possible reasons for the widespread polygyny in this population and the benefits of polygyny over monogamy for each sex (Plate 8). In particular, the sex

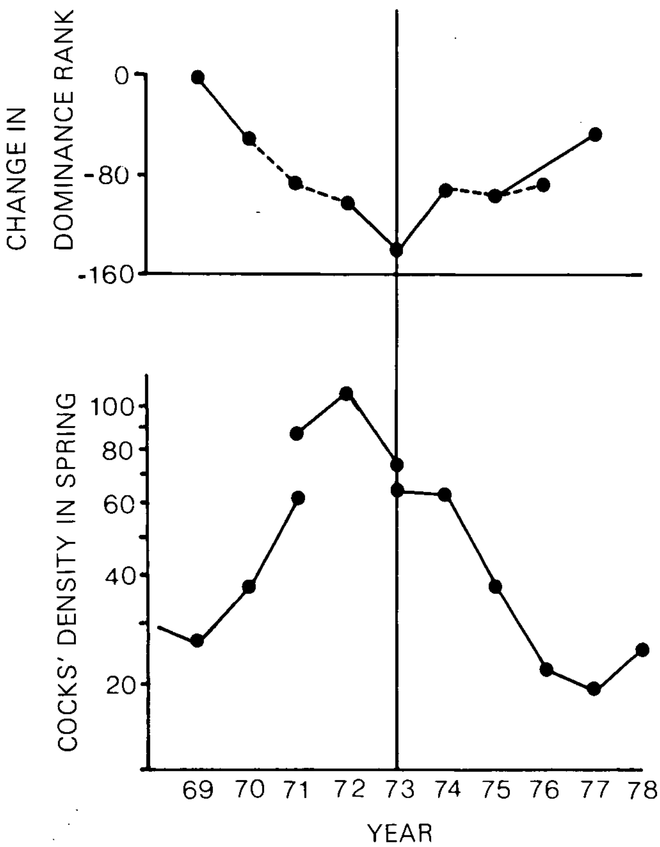

Figure 24 Annual changes in population density (cocks km^{-2} bottom graph) in relation to changes in the dominance rank. The gaps in the lower graph in 1971 and 1973 reflect minor changes in the areas from which eggs were taken. Solid lines in the top graph indicate that the change in dominance was significant at the 5% level (binomial test, 2-tailed probability). In the top graph, the dominance of 1977 cocks was compared with that of 1975 cocks and not with 1976 cocks, because we did not have enough 1976 cocks in 1977.

ratio and survival of adults and their young were studied from observations of colour-marked individuals, and the breeding performances of monogamous and polygynous individuals of each sex were compared.

Polygyny is uncommon in birds. It is most often found in species which nest in food-rich environments, such as marshes (Orians 1969); the same species is usually monogamous in a food-poor environment. An explanation for this difference is that males defending territories with much food, or territories with many potential nest sites which have good cover and are close to rich feeding areas, are likely to attract more than one female. There is usually great competition among females for such males.

Although prey abundance was not measured, it was obvious that the fertile land of Orkney supported a greater variety of prey, such as rabbits (*Oryctolagus cuniculus*), voles (*Microtus arvalis orcadensis*), and small passerines, than the bleak acidic moorlands of north-east Scotland, where most male harriers are monogamous (Picozzi 1978). The number of females per male among breeders was consistently greater than has been recorded anywhere else, and averaged 2 females per male; on one occasion, a male was associated with 6 females. The incidence of polygyny in Orkney was exaggerated (but not necessarily caused) by a very uneven sex ratio in the adult population. There were at least 3 contributory stages at which this uneven sex ratio could have occurred:

1. There could have been a differentially higher mortality of the nestling males, which are smaller than nestling females. No evidence was found; the last of the brood to hatch was usually the first to die, irrespective of its sex (Picozzi 1980). Sex ratios at fledging have changed inexplicably, from a run of years with more females fledging in the 1950s and early 1960s (Balfour & Cadbury 1979) to parity or more males recently.
2. Significantly fewer males than females were seen in Orkney as yearlings, presumably because of greater emigration and/or a higher over-winter mortality of juvenile males. Either way, there was no evidence for a substantially greater immigration of males to restore the balance, so the sex ratio in Orkney was biased in favour of females by the time the birds were one-year old.
3. Studies of the subsequent survival of colour-marked adults from year to year have shown that the rate of loss of one-year old and older males (21–33% per annum) was much greater than that of females (11–20% per annum). The sex ratio of the total population of birds of one or more years old was estimated as 3·5 hens:1 cock. As the only alternative to polygyny for the majority of females was not to breed, there was considerable competition among them for a mate and a nest territory.

The main advantage for males of pairing with more than one female was the likelihood that at least one of their mates would rear young, ie polygynists were more certain to rear young than monogamists. However, the mean number of young reared by males paired with 2 or more females did not increase proportionally with the number of females in the harem, because it was uncommon for more than 2 females of a group to rear young. Females were seldom able to rear young unaided, because there were so many avian predators capable of eating unguarded eggs and small chicks. Also, the weather was often cool and wet in June when the young hatched, and they could chill in 30 minutes if left unattended.

The mean number of young reared by successful females associated with monogamous or polygynous males was the same, so that, in this respect, females paired singly or as one of a harem were similar. However, not all females reared young, and, as harem size increased, a greater proportion of females bred unsuccessfully. Generally, the first to lay were the most likely to be successful, because their young hatched first and the attention of the male at that critical period was more certain.

N. Picozzi

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EFFECTS OF HUMAN IMPACT ON PTARMIGAN AND RED GROUSE NEAR SKI LIFTS IN SCOTLAND

Ski lifts and other facilities for downhill skiers have caused vegetation damage, soil erosion and scarring of the ski slopes in many countries, including Scotland (Bayfield 1971). Soil erosion on bared ground can be reduced by grass reseeding. However, many conservationists and bird watchers have been concerned at the possibility that the interesting arctic-alpine birds on the ski slopes and adjacent high ground are at risk (2 National Nature Reserves lie close to the ski grounds at both Cairn Gorm and Cairnwell).

Watson (1979) showed that the population density and breeding success of the native ptarmigan and red grouse did not differ significantly between areas visited by numerous people on the ski grounds and nearby areas visited by very few people. This result applied to both Cairn Gorm and Cairnwell. Scavenging crows are aliens to the arctic-alpine zone, but have probably been attracted there by food scraps left by the many tourists, and their numbers have increased on heavily visited study areas, and, to a lesser extent, on the nearby lightly visited areas also. Crows were found to have robbed the eggs of ptarmigan and other native birds, and the influx of these scavengers was thought to pose a new threat to hill birds in this area.

In 1981, it was noticed from the tables in Watson (1979) that, although the above conclusions from that paper remain unchanged, nevertheless the breeding success of ptarmigan and red grouse was extremely low on all the study areas at Cairn Gorm. In 5 out of 10 years, no young ptarmigan at all were reared, and the mean annual production for the 10 years was only one or 2 young per 10 adults. Added to this conclusion, in all 3 years when grouse breeding was measured at Cairn Gorm, no young were reared. With such poor breeding success, none of the stocks on these areas could have maintained itself without heavy immigration from more productive populations outside. As this low success occurred on areas seldom visited by people just as much as on the nearby heavily visited areas, direct human disturbance and indirect effects such as trampling leading to vegetation damage and soil erosion can be ruled out. The most likely explanation is that egg robbing, and perhaps chick robbing, by crows was sufficiently heavy to depress breeding success greatly on all the study areas.

This suggestion of a new factor, concentrated on, and near, the ski slopes, is strengthened by past data from Cairn Gorm, showing better breeding success before the ski developments, and by recent data from other parts of the Cairngorms showing similarly better breeding during the same years as the recent poor breeding on Cairn Gorm. The breeding success of both ptarmigan and red grouse has remained good at the Cairnwell ski grounds and on nearby areas little visited by people. The data in Watson (1979) show that crows have been much scarcer there than at Cairn Gorm, and, in the last few years, they have been absent at Cairnwell.

In late winter and spring 1981, a high proportion of ptarmigan and some grouse died from flying into the wires on chair lifts and ski tows at Cairn Gorm. By May, the ptarmigan stock in Coire Cas, the most developed part of the ski grounds, had become extinct. The wires have killed ptarmigan and grouse at Cairn Gorm and Cairnwell annually since the first lifts were made, but, in the earlier years, these deaths had no effect on stocks (Watson 1979). However, the number and length of wires have greatly increased as new lifts have been added, especially in 1980, and the length of wires per unit area is now higher in Coire Cas than anywhere else. Another associated factor is that Coire Cas has more skiers than Cairnwell, and so the ptarmigan there are more likely to be flushed by skiers than at Cairnwell, with a consequent greater risk of hitting the wires before they land.

A. Watson

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Animal Function

TESTIS DEVELOPMENT IN YOUNG RABBITS

The wild rabbit (*Oryctolagus cuniculus*) is a strictly seasonal breeder, with the first young being born in January and the last in late summer. Young born at the start of the season undergo early puberty and grow their gonads in response to some favourable environmental stimulus. As can be seen from Figure 25, young males

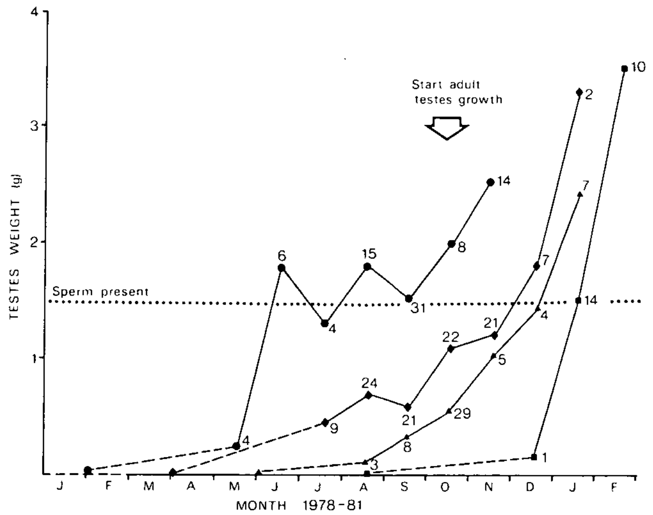

Figure 25 Paired testes weight for young animals shot in the vicinity of Monks Wood. Period of birth was determined for each animal by extrapolating its age, knowing its body weight, from a growth curve. Number of animals in each sample is indicated. Histological examination indicates the presence of sperm in testes weighing over 1·5 g.

born in January or February undergo rapid sexual development, with the appearance of mature sperm by 5 months of age. The final maturation of the testes and growth to adult size begin in October or November. Young born after February show a delayed puberty. Testicular growth is very slow, and no sperm are present until December or January when the final maturation of the testes also begins. It appears that these animals were too young in the spring to respond to the favourable environmental stimuli, so testicular development was delayed until the next breeding season, when some animals were approaching 10 months of age.

Most wild European mammals use daylength as an environmental cue to regulate their breeding cycles. Animals like the vole breed in response to lengthening days, while the sheep's breeding cycle is initiated by short winter daylengths. Little is known of the photoperiodic response of the wild rabbit, but the results shown in Figure 25 suggest that testis growth is stimulated by increasing daylengths.

Testis growth is regulated by 2 hormones, luteinizing hormone (LH) and follicle stimulating hormone (FSH), produced by the pituitary gland and released into the blood. The blood concentration of LH in the male rabbit is low, and apart from some erratic fluctuations during the first few months of life, when the animals were still immature, no significant change was observed during the period of study (Figure 26). FSH appears to be the hormone totally responsible for stimulating testis growth and development in the rabbit. The significant increase in plasma FSH concentration between January and February/March in both years stimulates testicular growth and heralds the start of the new breeding season. During the first season, blood FSH concentration remains high until May, after which it returns to the non-breeding level. Testicular collapse begins from June onwards. FSH secretion appears to begin earlier during the second year of life, and testicular growth is greatly increased. If the normal pattern of FSH secretion is disrupted by placing animals on a fixed 16 hours light:8 hours dark photoperiod, the seasonal change in testis weight and sexual development is also disrupted (Figure 27).

D. T. Davies

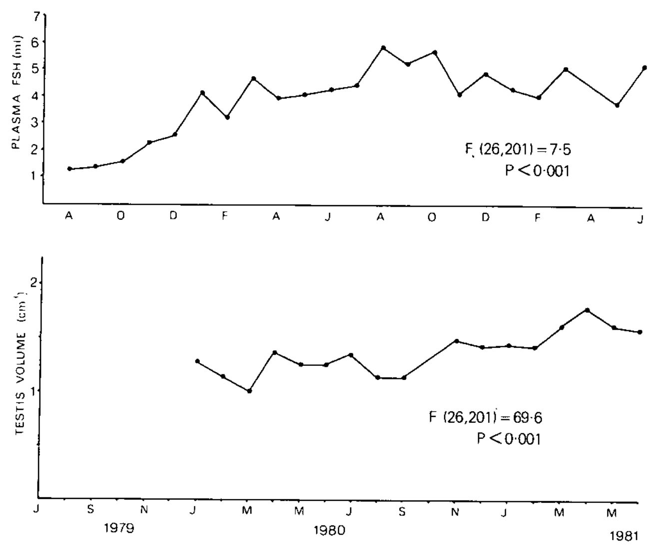

Figure 27 Rabbits born in May were transferred at 6 weeks of age to a fixed photoperiod of 16 h light:8 h dark and bled every 2 weeks for 23 months. Both plasma FSH and testis volume showed a significant increase over the duration of the experiment, but no seasonal pattern was observed. Throughout the period, the testis volume was significantly less than that for males on the natural photoperiod (cf Figures 26a and c).

REPRODUCTIVE EFFORT IN THE COMMON FROG (*RANA TEMPORARIA*)

Although everyone is familiar with the early part of the frog's life cycle, very little is known of its adult life or population dynamics. This project is aimed at providing fundamental information about reproduction, mortality and dispersal which can be used to draw up guidelines for the conservation of frog populations.

One approach is to examine the ways in which frogs divide up their assimilated resources among the possible activities of growth, maintenance, storage and reproduction. Storage is an important factor, as the frog must provide for a period of winter dormancy followed immediately by costly reproductive activity.

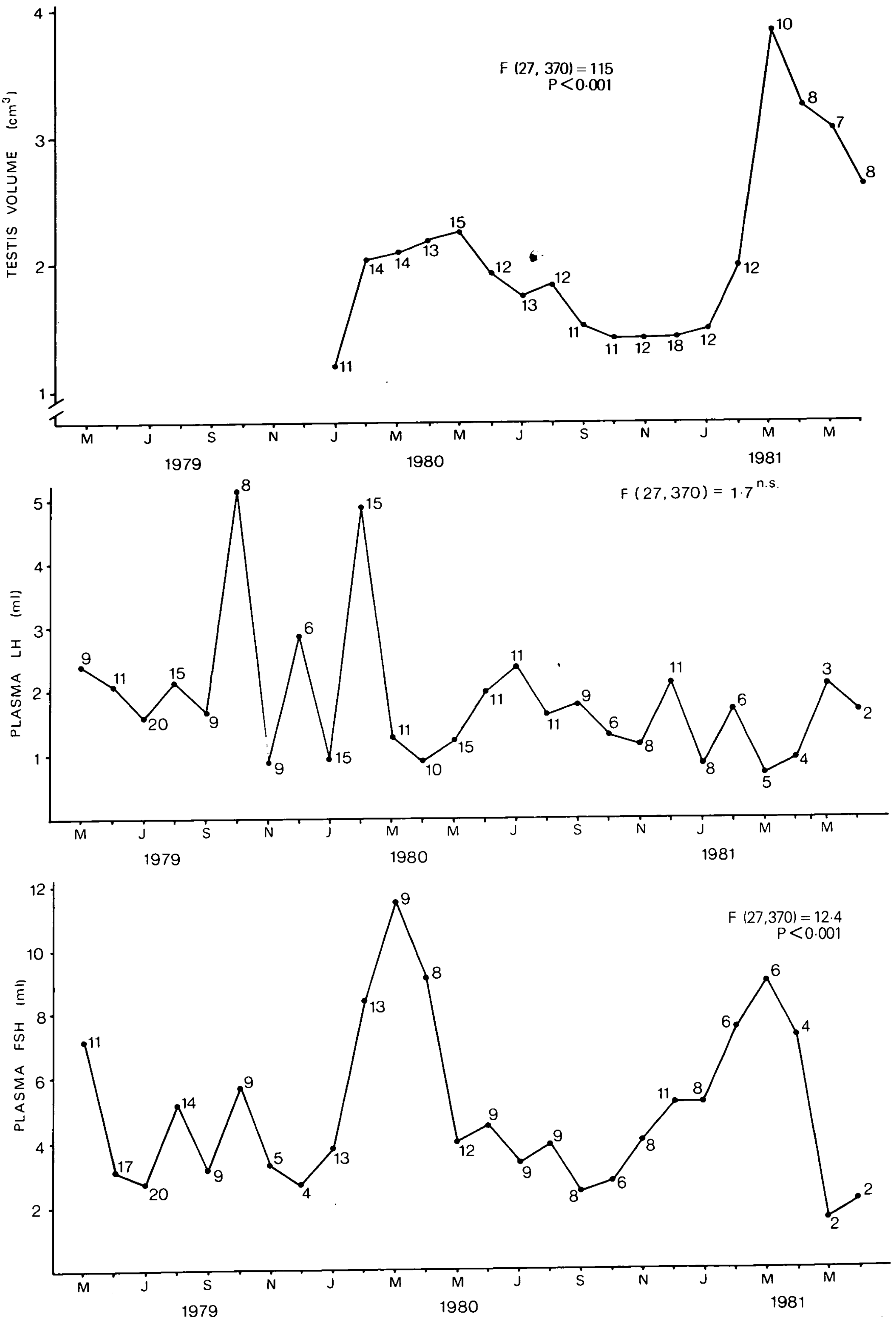

Figure 26 *Rabbits born in either March or April into the enclosure at Monks Wood were bled and examined every 2 weeks for 26 months. (a) Calipers were used to determine the width (w) and length (l) of the testis and the volume was determined using the equation: Vol = $\pi w^2 l/4$. (b) and (c) Plasma LH and FSH were determined using a radioimmunoassay.*

Growth exerts an influence through size, which can affect the frog's vulnerability to predators, the range of prey and refuges available to it, and its reproductive potential. A female's capacity for carrying eggs increases with body size, and it has been demonstrated for toads, which have similar mating behaviour, that largeness is advantageous to males in combat for females (Davies & Halliday 1977).

Early results of a long-term study of a wild population and a single comparison with an introduced suburban colony have demonstrated differences in the number of eggs in a frog's ovaries before and after hibernation and between sites (Figure 28). Frogs were collected from ponds at the Saltfleetby NNR, Lincolnshire, where they were hibernating in submersed holes in the banks. The ovaries were dissected out and samples taken to determine water and lipid contents, and the number and mean diameter of eggs. Other components of the frog carcases were similarly analysed, and 4 (male) or 5 (female) tissues were screened for DDT (or DDE) residues. No DDT or DDE was detected. Analysis revealed a significant decrease in the dry body weight of frogs between the November and February Saltfleetby samples. The dry weight of the ovary declined similarly, and there was no overall change in gonosomatic index (dry ovary/dry frog minus ovary), which ranged in individuals from 18·4% to 42·1%. The number of eggs per frog (fecundity) decreased between samples, while mean egg diameter, which increased with frog length (Figure 29), remained unchanged. Fecundity in the garden sample, taken in March, was higher than that in the November Saltfleetby sample. Regression coefficients of fecundity on length did not differ between populations. In most cases, fat bodies were depleted by November and showed no decline over winter. It appears, therefore, that the primary function of the fat bodies is to support gonad maturation, and that over-winter maintenance is at the expense of somatic and gonadal tissue. Gonadal decline occurred by reducing fecundity, the size and lipid content of the eggs showing no significant change. An alternative explanation of the decrease in mean fecundity is that mortality was greater among highly-fecund frogs, but this seems less likely as the gonosomatic index did not decline. The importance of egg size has yet to be determined, but it seems reasonable to expect that large eggs will, in some circumstances, be more valuable than small eggs, perhaps by giving rise to larger tadpoles or by surviving longer when temperature is low and development slow. Large, old frogs might thus make an important contribution to the survival of a population when conditions are poor, even though they may be few in number.

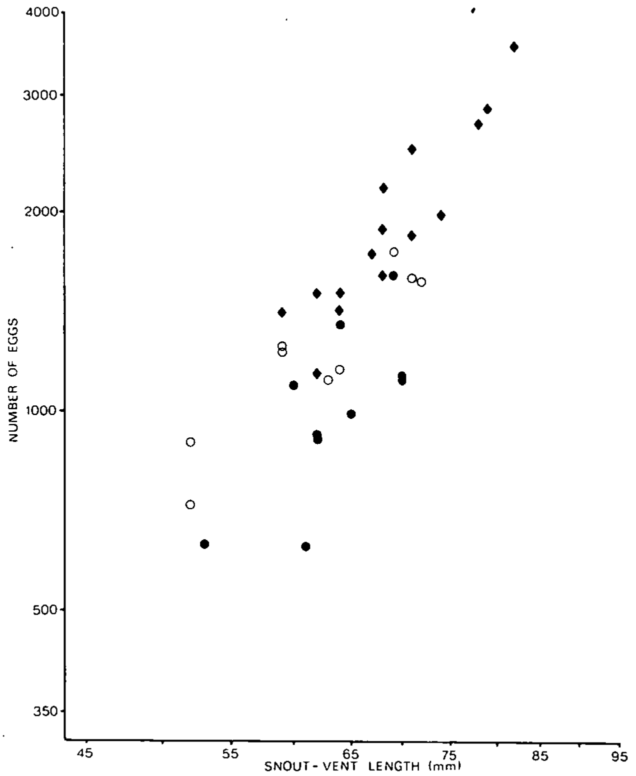

Figure 28 Log-log plot of numbers of eggs in the ovaries of frogs from Saltfleetby NNR (○ November 1980; ● February 1981) and eggs laid by frogs from a garden pond in Cambridgeshire (◆). Sample means, adjusted for frog lengths, are significantly different, but slopes are homogeneous and do not differ significantly from 3.

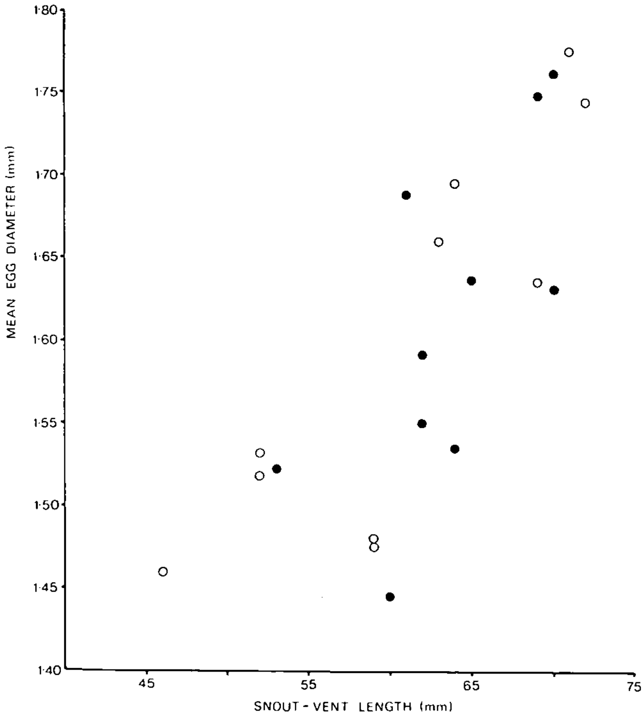

Figure 29 Mean diameters of eggs from 2 samples of frogs from Saltfleetby NNR (○ November 1980; ● February 1981). There is no significant difference between adjusted sample means.

Current research on reproductive effort is directed towards identifying the main factors underlying differences between populations. Are these genetically based, each population being adapted to local conditions, or have they arisen from local environmental differences acting on an animal whose strategy is to be flexible? It is important that these questions are answered, if conservation measures are to be effective in the long term.

C. P. Cummins

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POLYMORPHISM IN ARCTIC SKUAS

Arctic skuas (*Stercorarius parasiticus*) are seabirds belonging to the family Stercorariidae, and related to the gulls. In Britain, they are most commonly seen in spring and autumn, migrating along the west and east coast during their annual journey from wintering grounds in the southern oceans to their breeding grounds in the far north. Arctic skuas have a distinctive plumage polymorphism, and birds may be classified into 3 plumage types: pale, intermediate and dark. This colour variation is genetically determined largely by 2 forms, or alleles, of the same gene (O'Donald & Davis 1959). Only one allele produces melanism. Dark phases have 2 melanic alleles, pales have 2 non-melanic alleles, and intermediates have one melanic and one non-melanic allele.

There is a well-defined cline in the frequency of the melanic allele in breeding populations, with pales predominating in the northern colonies and darks in the more southern colonies. In the colony on Fair Isle, Shetland, which consists of 120 breeding pairs, only 21% of birds are of the pale phase. This colony has been studied intensively for many years in order to establish what selective forces are involved in maintaining the frequencies of the different colour phases. In particular, the colour combinations in breeding pairs were recorded carefully because, if there was any advantage in being one colour rather than another, the choice of mate would be crucial, as this would affect the colour of the offspring. The choice is especially critical in skuas because these birds are monogamous and retain the same mate year after year. Analysis of the choice of mate of many individually ringed birds has shown that mating is not random within the population: some females, irrespective of their own colour, prefer to mate with melanic males (O'Donald 1972; O'Donald *et al.* 1974); and some intermediate females prefer to mate with intermediate males (Berry & Davis 1970; O'Donald *et al.* 1974). Mating with darker males is advantageous, as these males breed earlier in the season and fledge more young per year. This greater production of melanics in a single season is counterbalanced by the greater number of breeding seasons experienced by pale birds, as they are, on average, 0·6 years younger than melanics when they breed for the first time (O'Donald & Davis 1975).

It has been assumed that melanism itself confers little physiological advantage on skuas, but that it may be genetically linked to some other character which does have direct physiological consequences. One approach to elucidate such a link is by the use of genetic markers, such as the variation in electrophoretic mobility of enzymes. Patterns of reproductive hormone secretion are also under genetic influence and will affect directly the birds' breeding competence. Studies on both isozymes and reproductive hormones were made for the Fair Isle skua population.

Two breeding seasons were spent on Fair Isle collecting blood samples and also maintaining both the programme of individual colour ringing and the records of breeding success for every nesting pair. It was fairly simple to catch nesting adults, as most of them would enter a funnel trap placed on the ground over their nests. However, it proved impossible to catch adults before they began incubating, despite repeated attempts using different methods. A blood sample was taken from the wing vein of every adult caught and from any chick more than 14-days old. These samples are now being analysed as part of a joint PhD project between ITE and the University of Cambridge.

Jane French

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ORGANOCHLORINE POLLUTANTS IN SEABIRDS FROM ST KILDA

Restrictions on the use and disposal of organochlorine insecticides, such as DDT and dieldrin, have been in force for a number of years, but, for many reasons, these chemicals are still in widespread use in many areas. Even in the UK, the latest figures show use of DDT to be increasing, as some of our biological monitoring programmes have suggested. Similarly, despite restrictions on use and disposal, polychlorinated biphenyls (PCBs) – chemical relatives of DDT and dieldrin, originating from industrial and commercial uses – remain high in some animal tissues.

Both PCBs and the organochlorine insecticides have been shown to be toxic to wildlife, and many species spend some time in parts of the world where such insecticides are used, or where they may become contaminated with PCBs. Accordingly, the Institute is maintaining a watch on the concentrations of organochlorine compounds in British wildlife.

Part of this programme involves measuring these compounds in seabirds, as many internationally important breeding colonies occur around the coast of Britain. To obtain some measure of the background level of organochlorines in live birds far removed from local sources of pollution, birds were collected from the St Kilda island group, which lies about 80 km west of the Outer Hebrides.

The birds were collected just after egg laying in 1976 and 1977 – as part of a study described more fully by Freestone *et al.* (in prep.) and Osborn *et al.* (1979). All birds were thought to be members of breeding pairs and seemed healthy. Three species were examined: the puffin (*Fratercula arctica*), the Manx shearwater (*Puffinus puffinus*), and the fulmar (*Fulmarus glacialis*). Several tissues were analysed from each bird as this helps to identify which tissues are at risk from the chemicals and indicates whether exposure has been chronic or acute. Table 24 summarises the levels of organochlorines found in liver, muscle, kidney, and fat.

Of the dozen or so organochlorine chemicals that might have been found in the birds, only 2 were present in detectable amounts. These were DDE (the stable metabolite of DDT) and PCBs. One puffin liver may have contained a very small quantity of dieldrin. The concentration of PCBs was higher than that of DDE in all species and tissues, except for the fat of 1977 Manx shearwaters.

For PCBs, there was little evidence of between-year variations in the mean concentrations, except in the case of fulmar kidneys where the 1977 value is at least 7 times that for 1976. An explanation for this peculiarity could lie in physiological, or pathological, events associated with the high metal levels in these kidneys (Bull *et al.* 1977; Osborn *et al.* 1979). Year-to-year variations in DDE concentrations were evident, 1977 residues being higher in all cases, except in the kidneys of all species and the livers of puffins, where levels were too low to detect clear trends.

PCBs were more evenly distributed amongst the tissues than DDE. Kidney contained the lowest concentrations of both PCBs and DDE, while muscle and liver concentrations of the compounds were of the same order, and fat had the highest concentrations in all cases, except in the 1977 Manx shearwaters. Here, while the general rule applied to DDE, PCB concentrations were higher in muscle than in liver or fat. For the most part, the inter-tissue distribution pattern was consistent with the view that the birds had been chronically exposed to the pollutants through their diets. Of the 3 species, the fulmar was the most contaminated and the puffin the least.

Recent experimental work in both laboratory and field helps the interpretation of the significance of these residues of toxic chemicals. Walker (1980) showed that puffins have very active liver enzymes capable of metabolising organochlorines, which could explain why puffins are relatively uncontaminated. Harris and Osborn (1981) obtained concentrations of PCBs in dosed puffins far higher than those recorded for these birds, but observed no discernible effect on survival or breeding, which suggests that these animals are at little risk from the organochlorine concentrations found in their tissues on St Kilda. Much less directly relevant

Table 24. DDE and PCB residues mg (chemical) kg^{-1} (dry weight tissue) in 3 species of St Kildan seabirds

			DDE					PCB			
Species	Year		Liver	Kidney	Muscle	Fat		Liver	Kidney	Muscle	Fat
Puffin	1976	Mean	0·07	<0·04	<0·10		Mean	3·81	2·87	4·73	
		Range	0·05–0·11	ND–0·05	ND–0·11	na	Range	1·82–5·04	0·53–4·12	3·63–6·07	na
		n	3	3(1ND)	3(1ND)		n	3	3	3	
	1977	Mean	0·08	ND	2·41	10·5	Mean	2·82	1·37	1·98	21·1
		Range	ND–0·08	–	1·11–3·08	5·52–23·5	Range	0·28–10·9	0·33–2·95	0·68–3·69	4·20–51·0
		n	9(8ND)	9(9ND)	10	9	n	9	9	10	9
Manx shearwater	1976	Mean	0·09	<0·07	0·16		Mean	3·98	2·07	6·74	
		Range	0·07–0·12	ND–0·09	0·10–0·18	na	Range	3·62–4·81	1·86–1·99	2·33–10·0	na
		n	4	3	4		n	4	3	4	
	1977	Mean	<2·73	ND	4·63	6·36	Mean	3·68	2·13	9·64	4·57
		Range	ND–6·98	–	3·07–5·46	4·05–7·99	Range	0·58–7·20	0·59–3·68	8·48–13·0	1·68–8·32
		n	4(1ND)	4(4ND)	4	3	n	4	4	4	3
Fulmar	1976	Mean	3·02	1·67	2·75		Mean	16·0	<3·03	19·6	
		Range	1·43–4·40	1·09–2·37	0·57–5·48	na	Range	3·59–32·7	ND–3·03	6·04–39·2	na
		n	4	3	4		n	4	3(2ND)	4	
	1977	Mean	9·52	<1·10	6·52	10·1	Mean	18·4	20·2	20·1	42·7
		Range	3·05–18·2	ND–1·10	4·87–9·20	6·55–14·5	Range	4·47–56·3	3·22–64·1	10·2–28·3	21·7–76·2
		n	5	5(4ND)	5	5	n	5	5	5	5

Notes: Some means are shown as <x mg kg^{-1}. In these cases, some non-detected (ND) analytical returns were made, and a mean has been calculated using the results for those samples where the chemical was detected. The true mean is thus less than the calculated value and is shown as such in the table; the number of non-detected values reported is given in parentheses. Typical non-detected values would be: DDE <0·02 mg kg^{-1}, PCB <0·2 mg kg^{-1}. na = not analysed.

experimental evidence is available for the shearwater and fulmar, although neither contain sufficient concentrations to give immediate concern for survival. However, some subtle effect of the higher concentrations found in the birds cannot be ignored.

Of some immediate concern is the apparent rise in DDE residues between the 2 years, a trend which, if continued, could lead to reduced breeding success, as the DDE could initiate egg-shell thinning in susceptible species. Further work is planned to check on the current DDE residues.

D. Osborn

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POLLUTANTS IN GUILLEMOT EGGS

Many of the persistent chemicals used in agriculture eventually find their way to the sea, along with others from various industrial effluents. They may then contaminate marine life, including seabirds. As part of our programme for monitoring pollutant residues in wildlife, we have been examining samples of seabirds and their eggs from different points around the coast for some years. In 1980, we made a particular effort to obtain guillemot (*Uria aalge*) eggs for analysis, because it was then about 10 years since a previous survey of this species. We hoped that the eggs would reveal geographical differences in pollutant burdens, and, at the same time, show whether any reductions in residues had occurred since the previous survey (Parslow & Jefferies 1975). Ten eggs were collected from each of 5 colonies, on Skomer Island (south-west Wales), Scare Rocks (south-west Scotland), St Kilda (north-west Scotland), Fair Isle (northern Scotland), and Isle of May (south-east Scotland). The number of eggs was limited by the costs of analysis, and also by the desirability of minimising disturbance of the breeding colonies. Three of the colonies (Skomer, Scare Rocks and St Kilda) had been sampled in the previous survey in 1969–1972, and the other 2 were close to colonies previously sampled. The pollutants of concern were DDE (from the insecticide DDT), HEOD (from the insecticides aldrin and dieldrin), PCBs (industrial polychlorinated biphenyls), and the heavy metals, mercury and cadmium.

Within these various eggs, DDE concentrations were mostly less than 2 ppm in wet weight (Figure 30). HEOD concentrations were mostly less than 0·5 ppm, and none was detected in any of the 10 eggs from St Kilda. PCB concentrations were mainly in the range 1–10 ppm. Residue concentrations seemed to vary somewhat between colonies, but only for mercury was this variation statistically significant ($F = 29{\cdot}3$, $P<0{\cdot}001$). Mercury seemed to be higher in eggs from the Irish Sea colonies than elsewhere, and, in the sample available, Scare Rocks showed no overlap with the rest (Figure 30). No cadmium was found in any eggs.

In the 3 colonies sampled on both occasions, some significant reductions in residues were apparent, comparing geometric means (Table 25, Figure 30). These included DDE, HEOD and PCB at Scare Rocks, and mercury in all 3 colonies. Moreover, the concentrations of most of these pollutants were lower in the other colonies sampled in 1980 than they were in the next nearest colonies sampled in the previous survey. On the other hand, DDE had increased significantly in eggs from St Kilda, although, on both occasions, the levels were low.

The declines in pesticide residues were consistent with known reductions in agricultural usage, especially of aldrin and dieldrin, in the 1970s. Declines in PCBs were consistent with restrictions in industrial use, and decline in mercury with its reduction in industrial effluent. It seems, therefore, that various government efforts to reduce environmental contamination by these particular chemicals have already had some measurable effect.

Table 25. Geometric mean (ppm) range (range of values within 1 standard error) of pollutants in guillemot eggs collected in 1969–72 and in 1980. T-tests indicate significance of difference between the 2 periods: ** P<0·01; ***P<0·001; NS not significant

	Skomer 1969–72	Skomer 1980	t-test	Scare Rocks 1969–72	Scare Rocks 1980	t-test	St Kilda 1969–72	St Kilda 1980	t-test
DDE	1·57 (1·41–1·75)	1·01 (0·81–1·26)	$t_{16} = 5{\cdot}21$ ***	1·71 (1·51–1·94)	1·23 (1·16–1·32)	$t_{23} = 7{\cdot}93$ ***	0·60 (0·55–0·65)	0·99 (0·81–1·22)	$t_{12} = 4{\cdot}04$ **
HEOD	0·05 (0·03–0·10)	0·01 (0·003–0·02)	$t_{16} = 0{\cdot}09$ NS	0·08 (0·06–0·10)	0·002 (0·001–0·004)	$t_{13} = 0{\cdot}29$ NS	0·003 (0·002–0·004)	0	$t_{26} = 0{\cdot}01$ NS
PCBs	8·50 (7·35–9·83)	2·35 (1·17–4·71)	$t_{9} = 19{\cdot}92$ ***	12·52 (10·50–14·92)	5·45 (4·69–6·33)	$t_{25} = 63{\cdot}3$ ***	0·49 (0·26–0·93)	1·52 (1·13–2·05)	$t_{19} = 3{\cdot}36$ **
Hg	4·37 (4·03–4·73)	1·04 (0·87–1·26)	$t_{12} = 37{\cdot}66$ ***	8·05 (6·89–9·42)	2·94 (2·73–3·17)	$t_{11} = 74{\cdot}27$ ***	1·50 (1·31–1·71)	0·76 (0·69–0·84)	$t_{22} = 9{\cdot}44$ ***

Note: Degrees of freedom were calculated using the formula given in Bailey (1959) for the comparison of means of 2 samples where the variances were unequal.

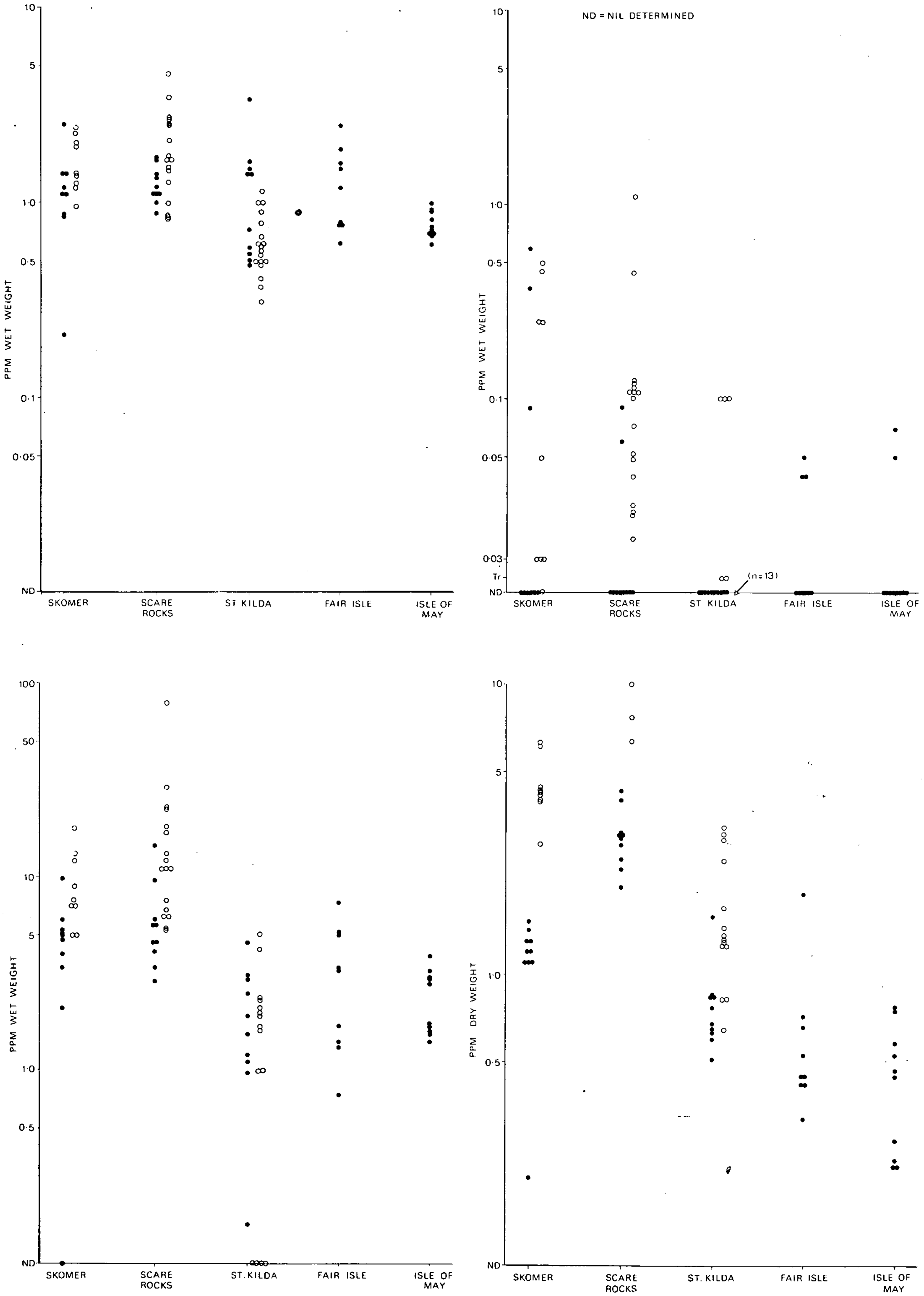

Figure 30 (a) DDE concentrations in eggs of guillemots in 1980 (●) and in 1969–72 (○). (b) HEOD concentrations in eggs of guillemots in 1980 (●) and in 1969–72 (○). ND = nil determined. (c) PCB concentrations in eggs of guillemots in 1980 (●) and in 1969–72 (○). (d) Mercury concentrations in eggs of guillemots in 1980 (●) and in 1969–72 (○).

The increase of DDE and PCB at the remote colonies on St Kilda may have been because these chemicals were more widely dispersed from their sources than at the previous survey, but on both occasions the levels were low and of doubtful biological significance. However, it would be useful to have more information on the year-to-year variations in levels, and further such analyses are planned. In both surveys, cadmium was below the detectable level in most eggs, but this metal is thought to be mainly natural in origin.

I. Newton, Margaret B. Haas and A. A. Bell

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FIDELITY TO TERRITORY AND MATE IN SPARROWHAWKS

As part of a wider study on sparrowhawks (*Accipiter nisus*) in south Scotland, information was needed on the turnover and mortality of breeding birds. Acquiring this information entailed trapping the occupants on as many territories as possible each year and identifying them from their ring numbers. The females were easier to catch than the males, and so more information was obtained for females. As in other parts of the country, sparrowhawks in the study area nested in the same places year after year. They built a new nest each year, near old ones, so that the nesting places could be recognised by groups of nests of different ages. From local knowledge, some of the places in our study area were known to have been used by sparrowhawks for periods of 40–50 years, in fact as long as the woods remained suitable.

For territories on which occupants were trapped in consecutive years, we examined whether the bird in the second year was the same individual there the year before, or whether it was a different individual. Of 58 territories where males were caught in successive years, on 25 territories it was the same individual in the second year, and on 33 territories a different individual; of 296 territories where females were caught in successive years, on 148 territories it was the same individual in the second year, and on 148 a different one. This gave annual turnovers for cocks of 57% and for hens of 50%, which were equivalent to mean residence periods of 1·4 years and 1·5 years respectively, with no significant difference between the sexes.

The above figures gave estimates of the mean turnover from year-to-year changes, but many birds were identified in several years, so that their full residence periods on particular territories were known (Table 26). Only those birds known to start and end their occupation of a particular territory within the 11-year study period were included. Such records were probably biased slightly in favour of short periods, because long periods were more likely to overlap the start and end of the study, and so be excluded, which may be why the mean periods of residence, at 1·3 years for both sexes, were slightly shorter than the means calculated above from the year-to-year changes. However, the data were interesting in showing the shortness of the periods involved. The majority of sparrowhawks retained the same territories for only a year or 2, and only occasional individuals for up to 4 years (cocks) or 6 years (hens). Hence, the long-term occupation of territories by this species was produced by many different individuals occupying the same territories in quick succession, each staying for a short time.

Table 26. Periods that individual sparrowhawks were resident on territories

	Residence periods (years) of individuals						Mean
	1	2	3	4	5	6	
Number of cocks	42	8	1	1	0	0	1·3
Number of hens	173	22	7	4	1	1	1·3

Part of the turnover was related to mortality: more than 30% of breeding sparrowhawks died each year, so that more than 30% of territories provided gaps for new recruits each year. In addition, however, some birds changed territory from one year to the next, so they too contributed to turnover. Of 32 males caught in successive years, 78% were on the same territory on the second occasion, while 22% had moved to a different territory. Similarly, of 215 hens caught in successive years, 69% were on the same territory, while 31% had moved to a different territory. These figures suggested that females changed territories more often than males, but the difference was not statistically significant. Most birds which changed territories moved only a few kilometres, but, in general, females moved further than males.

The tendency to change territory was related to previous nest success. Of 161 females which had bred successfully the previous year, only 22% changed territory, whereas of 54 females which had failed in their breeding the previous year 58% changed territory. The difference between the 2 groups was highly significant statistically (Table 27). A similar tendency was apparent among the males, but samples were smaller, and the trend not significant.

Table 27. Frequency of territory changes in relation to previous nest success, based on birds identified in consecutive years

	Cocks		Hens	
	Number	% changed territory	Number	% changed territory
After success	22	14%	161	22%
After failure	10	4%	54	58%

Table 28. Proportion of hens which changed territory, according to age and nest success in the previous year. Birds which failed the previous year changed territory more often than birds which succeeded, but the tendency to change territory became less marked with increasing age.

	Comparisons between the following ages					
	1 to 2		2 to 3		3+ to following year	
	Number	% changed territory	Number	% changed territory	Number	% changed territory
After success	11	45	21	24	129	20
After failure	10	100	9	56	35	46
Significance of variation within age groups	$x^2 = 5{\cdot}2$, $P < 0{\cdot}05$		$x^2 = 1{\cdot}6$, $P < 0{\cdot}3$		$x^2 = 0{\cdot}8$, $P < 0{\cdot}5$	

The tendency to move after a nest failure was especially marked between the first and second year of life in hens, and became less marked with age (Table 28). Older hens showed greater tendency to stay on the same territories, whether successful or not the year before. Among males, the sample of one-year olds was very small, but, among older birds, the same trend held as in hens, ie greater residency with increasing age.

The high mortality and movement meant that most sparrowhawks had a different mate each year. Some pairs remained together, however, and 4 years was the longest period that a pair was known to stay together on the same territory.

With such rapid turnover, we wondered whether previous experience of territory or mate influenced breeding success, and hence whether there was any advantage in birds remaining faithful in these respects from year to year. We therefore examined the breeding performance of 3 categories of pairs, ranked according to their previous experience. In one group of pairs (a), both partners had been together on the same territory in the previous year; in a second group (b), one partner had been on that territory the previous year, but the other partner was new; while in the third group (c), each partner was new, both to the territory and to one another. As may be seen from Table 29, previous experience and breeding performance seemed to be related, in that pairs in category (a) did better in all respects than those in category (c), while pairs in (b) were intermediate.

One might conclude from this result that previous experience of territory and mate affected breeding success. However, the situation was more complicated. In some pairs in category (b), the new partner was a yearling, while in some of those in (c) one or both partners were yearlings. As yearlings may have bred less well than older birds because of lack of experience as such, rather than through lack of experience of a particular territory or a particular mate, we therefore re-examined the data, excluding all pairs with yearlings. Again, the same trends held, with the more experienced pairs performing best.

In view of this last result, it was surprising that so many birds changed territory when the best breeding results were shown by birds which stayed put. However, further inspection of the data showed that quality of territory was involved, and, at any given age, birds more often moved from poor territories than from good ones. In consequence, it was chiefly on the good territories that pairs tended to stay together in successive years. There was thus no unequivocal evidence that previous experience of a territory was important to nest success, for the territories where birds stayed were of better quality anyway.

I. Newton and M. Marquiss

Table 29. Breeding performance in relation to previous experience of mate and territory

	Including yearlings				Excluding yearlings			
	Number	Mean laying date	Mean clutch size*	Mean brood size*	Number	Mean laying date	Mean clutch size*	Mean brood size*
(a) Same territory same mate	13	12 May†	4·4	3·0	13	12 May†	4·4	3·0
(b) Same territory new mate**	26	12 May	3·5	2·8	20	10 May	3·9	3·2
(c) New territory new mate	16	15 May	3·5	2·0	10	16 May†	3·2	2·6

*Includes zeros.

**Includes 13 cases where the cock was new, and 13 cases where the hen was new.

†The difference between these values was significant: $t_{16} = 3{\cdot}08$, $P < 0{\cdot}01$

KESTRELS IN FARMLAND

Research on kestrels (*Falco tinnunculus*) started at Monks Wood in October 1980, the aim being to study the numbers, home range and breeding success of kestrels in farmland and to compare these with similar data collected in young forestry plantations in south Scotland (Village 1981). A second aim is to see whether kestrels in farmland are polluted with organochlorine pesticides or with heavy metals, and to determine how the uptake of pollutant varies between individuals. Kestrels eat a variety of prey, such as small mammals, small birds, beetles and earthworms; different prey may carry differing amounts of pollutant, so individual kestrels eating mainly one kind of prey may be more or less contaminated than other individuals eating mainly different prey.

The first task was to find suitable places to work and to start answering the basic questions, such as how do kestrel numbers vary within and between years, and how do these variations relate to changes in prey numbers? Two similar-sized study areas have been chosen, one in fairly 'typical' mixed farmland in south Rutland, and the other in intensive arable farmland on the Cambridgeshire fens. The farms in Rutland are mainly arable, but contain numerous woods and hedgerow-trees (which provide most of the nesting holes), as well as significant areas of grazed permanent pasture. The fens, on the other hand, have few trees (and therefore few nesting sites) and virtually no livestock. Last summer, 34 breeding pairs were found in Rutland, but only 10 in the fens. This difference may disappear, if nest boxes are placed on the fens for extra kestrels to breed.

In any area, the breeding success of kestrels varies between years, so it is hard to interpret the results of only one breeding season. The mean laying date and clutch size in 1981 were similar to the worst year recorded in south Scotland (Table 30), although the proportion of breeding birds that were yearlings was similar to, or higher than, the best years in Scotland. It will be several more years before it is known whether these results are typical of farmland areas.

To determine how kestrels use their range, where they hunt and what they eat, a number of birds were fitted with radio transmitters, which enable individuals to be followed for long periods. Already, the importance of certain habitats can be seen for certain foods; for example, permanent pastures seem to be important sources of invertebrates. It is hoped to continue such monitoring in order to build up a picture of how the birds use farmland at different times of year and whether or not this use varies from year to year. Chemical analysis of different types of prey may also indicate which are most heavily contaminated, and so pinpoint the conditions under which kestrels are most likely to take contaminated prey.

A. Village

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ANNUAL CYCLE OF REPRODUCTIVE HORMONES IN THE FERAL PIGEON

In Britain, large populations of feral pigeons exist in every urban centre, and their numbers are sufficiently high for them to be regarded as pests in many cities. They are able to exploit the urban environment so well, partly because, compared with other free-living birds, they have an extremely long breeding season. This extension of the breeding season is possible because food is abundant over most of the year, and also because young pigeons are fed by their parents on crop milk, a nutritious liquid produced by the adult's crop wall. This means that, as long as there is sufficient food for the adults and newly-fledged young, breeding may be successful, which is in contrast with other birds who also have to provide their young with a high protein and high calorie diet, and who rely on food sources which are only seasonally abundant. In order to capitalise on this ability to rear young throughout the year, pigeons remain in a physiological state of readiness to breed, one manifestation of which is the absence of any significant regression of the testes in the male and their continuous production of sperm (Lofts *et al.* 1966).

As part of a study on the reproductive physiology of wild birds, changes were examined in the reproductive hormones in a bird such as the feral pigeon, which has a

Table 30. Breeding performance and frequency of yearlings in the breeding population in young conifer plantations in southern Scotland, compared with farmland in eastern England

Area	Year	Sample size	Mean laying date	Mean clutch size	% yearlings in the breeding population: Males	Females
South Scotland	1976	22	29 April	5·1	–	–
South Scotland	1977	26	12 May	4·6	4	20
South Scotland	1978	38	28 April	5·1	32	54
South Scotland	1979	43	1 May	5·1	15	49
East England	1981	28	14 May	4·5	32	32

long breeding season. The levels of reproductive hormones in the blood of non-paired pigeons (Figures 31 and 32) reflect this potential for extended breeding. All hormones, apart from progesterone, are elevated from February to the end of October, which is the period when most young are produced. Even outside this period, when few eggs are laid in the wild, hormones do not fall to the same low level as in other bird species. In male pigeons, the rise in plasma testosterone, which begins in late December, does not correspond to a renewal of testicular function and testis growth, as in other birds (Lofts *et al.* 1966). Testosterone is known to stimulate bowing behaviour, which signifies the initiation of courtship by the male. As the male produces sperm throughout the year, this early testosterone peak may therefore be of mainly behavioural significance. Interestingly, testosterone is elevated before there is any significant change in circulating luteinising hormone (LH) levels, because LH stimulates the production of testosterone, the major male reproductive steroid, by Leydig cells in the testis. Testosterone titre in the blood is monitored by the bird's central nervous system and inhibits further release of LH when the required level of circulating steroid is achieved. Such a simple feedback loop does not allow any changes in hormone level. To achieve a rise, or fall, in either LH or testosterone requires a change in the sensitivity of the feedback loop – either a testicular change, so that testosterone production rises, or falls, with the same LH stimulus, or a central change so that more, or less, steroid is required to inhibit LH release. The rise in testosterone before any rise in LH reflects a change in testicular sensitivity to LH, which then allows steroid output by the testes in pigeons to rise. This feature is in marked contrast to other birds, where LH secretion precedes a rise in plasma testosterone.

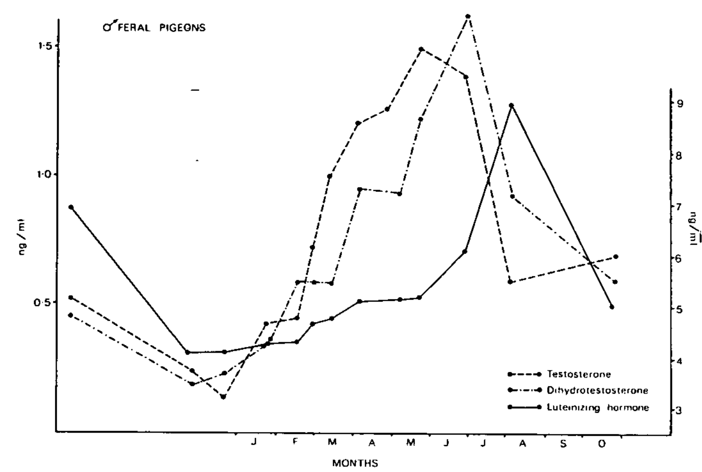

Figure 31 Seasonal changes in the concentrations of various hormones in the blood plasma of male feral pigeons.

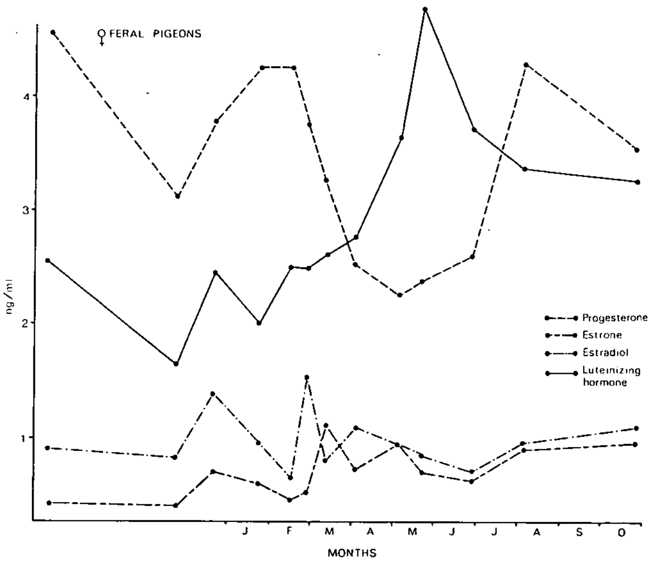

Figure 32 Seasonal changes in the concentrations of various hormones in the blood plasma of female feral pigeons.

From February to May, both LH and testosterone are rising, which indicates a change in central sensitivity to steroid feedback allowing a rise in circulating testosterone, without a decline in LH secretion. In June, testosterone begins to fall, despite a still rising LH titre, indicating a second change in peripheral sensitivity to the hormone. The rapid rise in LH at this time presumably reflects the falling steroid levels and the operation of the feedback loop. The fall of LH from August is caused by a change in central sensitivity (again lagging behind the change in testicular response which occurred 2 months earlier).

Dihydrotestosterone (DHT) is a metabolite of testosterone, and its appearance in the blood is a result of the breakdown of testosterone. Its levels therefore reflect those of testosterone.

In the female, the LH peak coincides with the male's testosterone peak, the highest point being about the summer solstice. There is an inverse relationship between LH and progesterone in female pigeons, and, during the breeding season, progesterone is low while LH is high. There is a slight rise in both estrone and estradiol following the rise in LH.

It is hoped to extend this work by studying the cause of the rise in testosterone in males which initiates the courtship behaviour that stimulates the female.

Jane French

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Plate 8 – Two female hen harriers sharing a nest in Orkney 1981, an exceptional example of polygyny.
Photograph N. Picozzi.

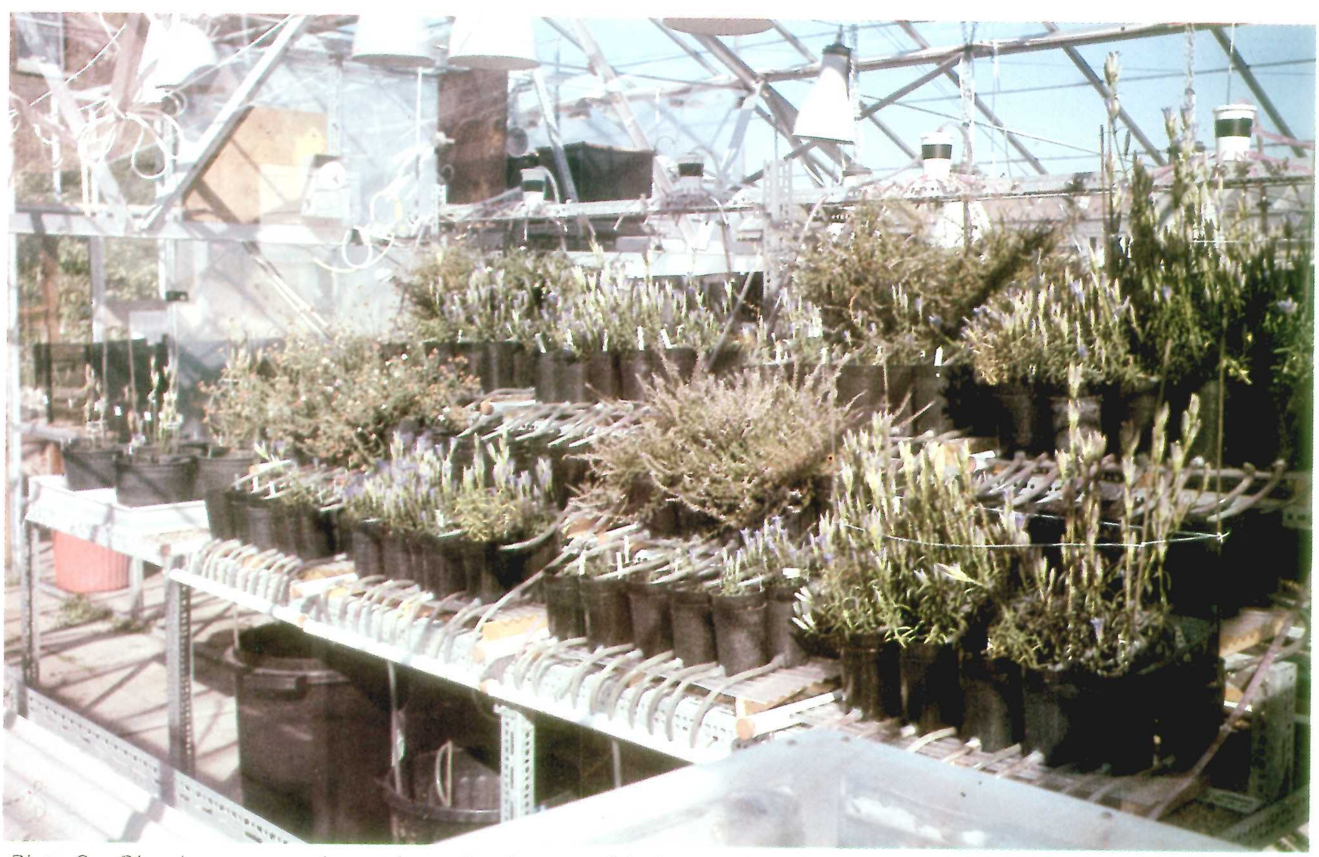

Plate 9 – Glasshouse experiment investigating possible interactions between plants of Gentiana pneumonanthe, Calluna vulgaris, Erica tetralix *and plant litter.*
Photograph S. B. Chapman.

Plate 10 – The Caledonian pinewood at Shieldaig, Wester Ross, shortly after a wildfire in March 1974, showing fire-damaged crowns of Scots pine.
Photograph J. M. Sykes.

Plate 11 – 'Graveyard' effect left after birch trees have been treated with a brush control herbicide.
Photograph R. H. Marrs.

SEASONAL CHANGES IN CORTICOSTERONE LEVELS IN STARLINGS

ITE is collaborating with the Institute of Virology in a project to determine, amongst other things, to what extent sublethal viral infections may cause stress in wild birds. The starling (*Sturnus vulgaris*) was chosen for this work because it is a common pest species and comparatively easy to catch in large numbers. As stress is known to cause an increase in the level of a hormone, corticosterone, in the blood of starlings, as in other species, it was possible to use the level of this hormone as a crude indication of the amount of stress to which a bird was being subjected. However, before any significance could be attached to a particular level of corticosterone, it was necessary to know the normal levels in wild starlings. This study aimed to determine these normal levels and how they changed during the year.

Free-living starlings were caught each month throughout 1980. During the breeding season, in April and May, they were caught using traps placed in nest boxes at Monks Wood. These traps were spring-loaded and triggered automatically by the birds as they entered the nest boxes. During the rest of the year, birds were caught in a mist net erected at a nearby sewage works, which was a favoured feeding place for starlings. In either case, blood samples were obtained from the birds within one minute of capture, and the concentration of corticosterone in the blood plasma was estimated by radioimmunoassay. The blood samples had to be obtained within one minute of capture because a previous study had shown that capture itself causes a large increase in corticosterone concentration and that this increase begins approximately one minute after capture.

The changes in plasma corticosterone concentration in male and female starlings during the year are shown in Figure 33. At no time did the levels in the 2 sexes differ significantly from each other. One of the effects of corticosterone is to promote the breakdown and mobilisation of energy reserves, particularly fats, and, for this reason, it was thought that changes in corticosterone levels may reflect changes in body weight. However, this does not appear to have been the case. Instead, it appears that corticosterone levels may have been associated with the degree of 'food stress' to which the starlings were subjected. There were 2 peaks during the year. The first peak was in May, and corresponded to the period when most starlings were feeding their nestlings. Although food was abundant at this time, the body weight of starlings decreased, possibly because they were very active throughout the day feeding the nestlings. The 5 months following May were associated with low corticosterone levels. Food was less abundant at this time, but less was needed because of the higher temperatures, and because the birds were no longer feeding young. Long daylengths ensure that an adequate supply can easily be found. From October onwards, starlings have to find more food in order to survive the colder weather, and sustain themselves over long winter nights. Consequently, corticosterone levels increased from October to a peak in December.

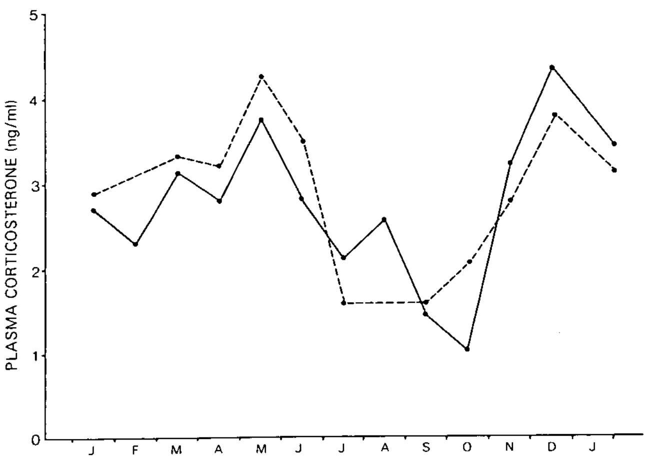

Figure 33 Plasma corticosterone concentrations in male (——) and female (------) starlings during the year.

A. S. Dawson

Plant Biology

BIOLOGICAL MONITORING OF THE FORTH VALLEY

Lichens and bryophytes growing on trees and walls depend almost entirely upon uptake of nutrients from rain water. This uptake is, however, non-selective and will include absorbed aerial pollutants which may be phytotoxic. Absorption of dry pollutants deposited directly on to the plant surface also takes place in moist conditions.

The appearance of, or increase in, concentrations of phytotoxic pollutants may result in the death of the plant, or at least in a reduction of its growth rate. Thus, it is possible to monitor changing concentrations of such pollutants by regular examination of the performance of selected species. It is clear, however, that a monitoring programme should take into account any change in growth rate due to other environmental factors, eg climate. The study area for the current programme comprises 7000 km^2 centred on the Forth Valley, and includes wide climatic and topographical ranges; therefore, a system of stratifying the study area has been devised, based on the land classification scheme developed within ITE.

The classification involved the compilation of topographical, climatic and geological features attributable to a 10% sample of the total number of kilometre squares. These data were extracted from Ordnance Survey, meteorological and geological maps. The analysis, based on the indicator species analysis devised by Hill *et al.* (1975), resulted in the production of 13 lowland and 6 upland land classes.

The recently completed primary survey involved visiting 10 km^2 from each of 10 lowland and 5 upland classes. The survey was designed to establish which lichen and moss species were potentially useful and to determine their current distribution, given that this distribution has already been affected by current and previous concentrations of pollutants, prior to establishing permanent monitoring sites.

The boles of unsheltered ash trees between $\frac{1}{2}$ and 2 m from the ground and the top surface of stone walls were selected as the most suitable substrates present throughout the study area, and 3 of each were examined in each designated km^2. The presence of all macrolichens (foliose: leaf-like procumbent, and fruticose: branched, erect or pendant types) was noted for each tree quadrant and 1 m length of wall-top, together with their percentage cover. Some of the resultant data for trees (in 3 upland and 3 lowland land classes) are represented in Figure 34, which shows that the most depleted flora generally exists within a strip 35 km wide running roughly south-west to north-east from Glasgow through the industrial complex at Grangemouth and continuing to the Fife coast. Clearly, however, Edinburgh is a source of pollution which contributes a local effect. This pattern is imposed regardless of land class and shows that the present macrolichen distribution has been determined by environmental factors other than those incorporated in the classification scheme. It is almost certainly due to the distribution of wind-borne pollutants, as prevailing winds follow the SW-NE bearing.

Further analysis is necessary to establish any difference between land classes but there are indications that, within the affected zone, macrolichens growing on trees in upland areas have a greater chance of survival. Opportunities for testing this hypothesis are restricted as most of the upland classes lie outside the most polluted zone, but the trees on higher ground east of Glasgow do support a greater percentage of macrolichen cover than nearby trees in lowland areas.

As the deleterious effect of SO_2 on lichens is well-known (although it is now believed NO_x may be equally damaging), and contoured SO_2 dispersion data (compiled by the Warren Springs Laboratory (WSL)) are available, it is possible to compare these data with the macrolichen distribution. Figure 34 shows that kilometre squares within or adjacent to the 50 $\mu g\ m^{-3}$ contour have been affected, but no more so than many localities far removed from these high SO_2 concen-

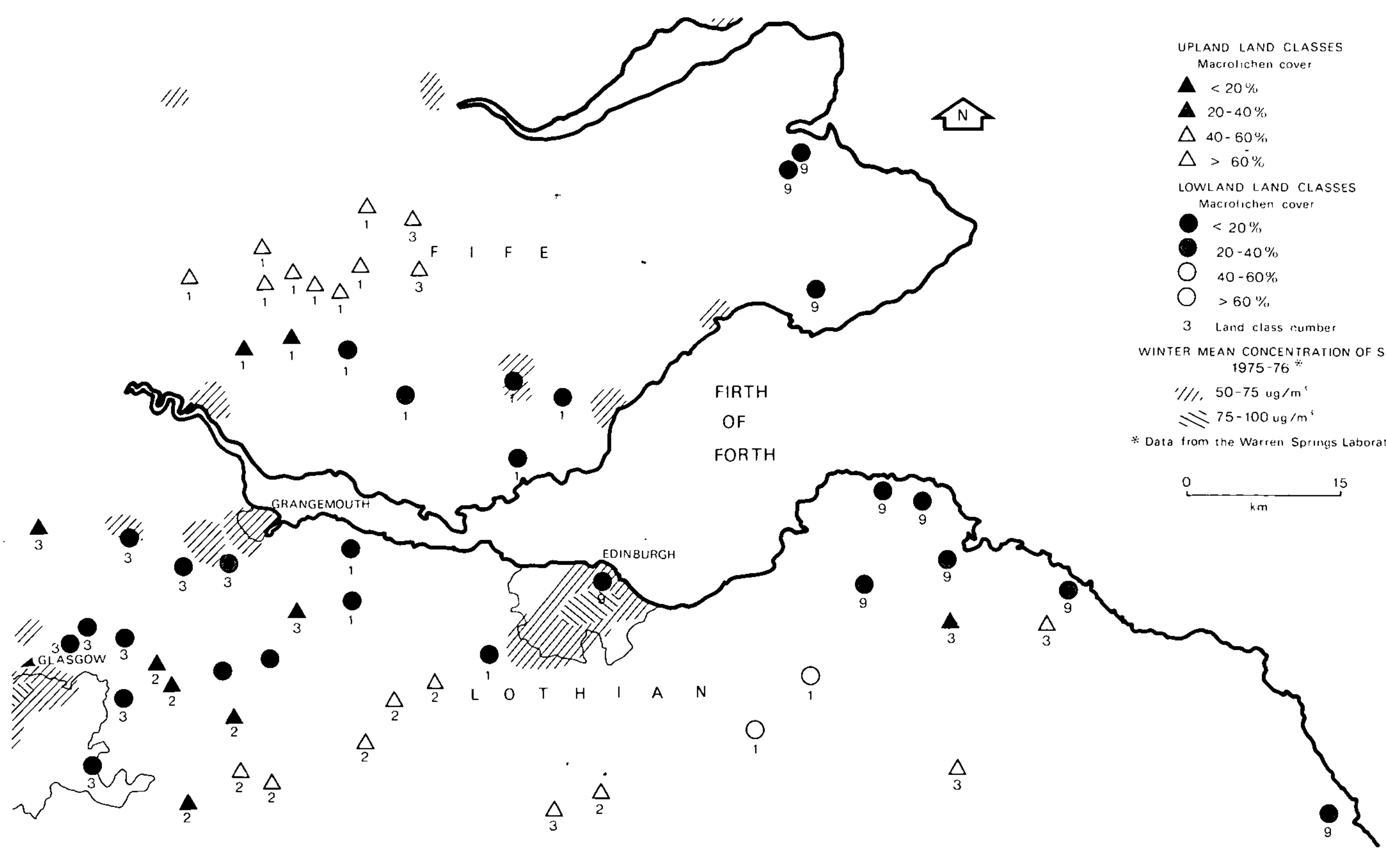

Figure 34 Map of the Forth Valley biological monitoring study area, showing distribution of macrolichens in 3 upland (1, 2, 3) and 3 lowland (1, 3, 9) land classes and the mean winter SO_2 concentration for 1975–76. Each symbol represents the mean total percentage cover of macrolichens, on the quadrant showing maximum percentage cover, of 3 ash trees situated in a square kilometre.

trations. Hawksworth and Rose (1970) published a quantitative scale linking the presence/absence of particular lichens with winter SO_2 concentrations, and the absence of macrolichen species from these localities indicates a far higher SO_2 concentration than indicated by the WSL contours. The main reason for these conflicting data is almost certainly that SO_2 concentrations have substantially decreased in the area, and the present macrolichen distribution is a reflection of earlier circumstances.

B. G. Bell

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'CROP' AND 'ISOLATION' IDEOTYPES IN FORESTRY

The relative performances of tree progenies are usually decided on the basis of mean individual tree heights or stem volumes at ages 4–10 after planting at about 2 m spacing, using experimental designs in which progenies are mixed together as single trees, in short rows, or small plots. In those circumstances, progeny rankings will depend (i) during the first few years, on their relative abilities to grow as widely-spaced individuals, ie on the degree to which they possess 'isolation' ideotypic traits enabling them to exploit the available space, and (ii) during the later years, on their relative competitive abilities, ie on the degree to which they possess 'competitive' traits enabling them to claim environmental resources at their neighbours' expense. At no stage will the experiments favour progenies which possess 'crop' ideotypic traits, defined by Donald (1968) as those which enable plants to use environmental resources of light, water and nutrients efficiently in conditions of inter-plant competition to give high yields per unit area of ground. An extensive agronomic literature shows that neither spaced plant performance nor competitive ability are necessarily related to stand yields: large rank differences occur depending upon whether genotypes are grown in pots, mixtures, or in pure stands. Indeed, selection that favours enhanced competitive ability can sometimes depress yields per hectare in closed stands.

A nursery experiment was set up to determine whether progeny tests of *Picea sitchensis* might be favouring 'isolation' rather than 'crop' ideotypes. Two provenance standards (Masset, Queen Charlotte Islands, and Hoquiam, Washington), 7 'superior' open-pollinated progenies (ie 10–30% taller than Masset at age 4–6 in forest progeny tests), and 3 'inferior' open-pollinated progenies were planted in a nursery and evaluated after 4 years in 2 designs. In the first design, the progenies were planted at 1·4 m spacing, so that they did not come into contact during the 4 years. This spacing would favour progenies with the attributes of 'isolation' ideotypes, with the expectation that the ranking at age 6 would be similar to that in the forest progeny tests (ie the 'superior' progenies would grow taller than the 'inferior' progenies). In the second design, each progeny was grown in a pure stand of 10 × 10 trees inside 2–3 border rows at 14 cm spacing, so that there was within-progeny competition after the first year, presumed to favour progenies with the attributes of 'crop' ideotypes.

When grown as widely-spaced trees, all 7 'superior' progenies (S1 . . . S7 in Figure 35) were significantly taller than Masset provenance – as they were in forest progeny tests – and 2 of the 3 'inferior' progenies were not significantly taller than Masset. By contrast, when the progenies were grown in closed stands, none of the 'superior' progenies grew significantly taller than Masset or 2 of the 'inferior' progenies. Indeed, one of the 'inferior' progenies was tallest. Similar patterns were found for stem diameters, basal areas, total above-ground biomass and stem biomass. There was no significant correlation between progeny performance as widely-spaced trees and performance in closed stands, whether calculated per tree or per hectare.

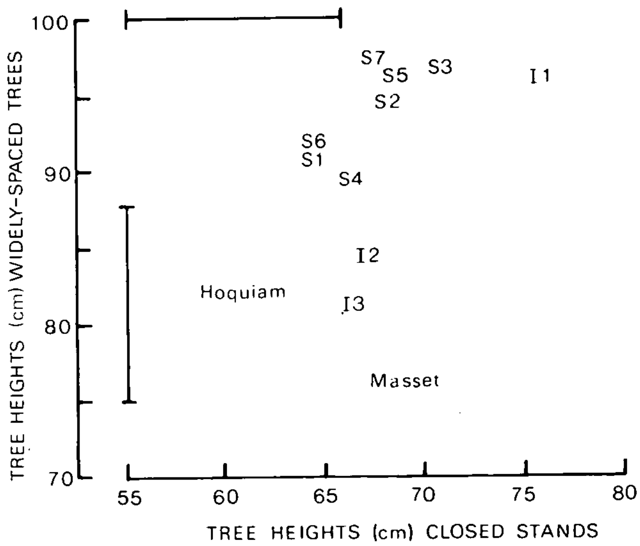

Figure 35 Mean heights of 12 populations of Picea sitchensis *(Masset and Hoquiam provenances, and 10 progenies) at age 4, when grown in a nursery as either widely spaced trees or in closed stands. 'S' – a progeny with superior height at age 4–6 in replicated forest trials relative to Masset. 'I' – a progeny with inferior height at age 4–6 in forest trials relative to Masset. The vertical and horizontal bars are least significant differences at P = 0·05.*

It was concluded that, under the conditions of this nursery experiment, the 'superior' progenies (as determined in forest progeny tests) did not use environmental resources efficiently in conditions of inter-tree competition. However, there was no evidence that they were inefficient, ie that selection for performance in isolation would depress current annual increments in biomass or volume per hectare in closed stands. Rather, the evidence was that selection in progeny tests at age 4–6 might be ineffective at increasing productivity per hectare after stand closure.

The implications for tree breeding are clear, namely that the normal process of progeny testing favours 'isolation' ideotypes, which will be 'superior' only as long as there is no appreciable inter-tree competition (perhaps during 30% of the rotation). Consequently, genetic gains calculated from progeny test data may overestimate actual genetic gains measured in terms of biomass or volume yield per hectare over a full rotation.

Unfortunately, there is little that a tree breeder can do to overcome this problem, because (i) it would be prohibitively expensive on heterogenous forest sites to test tree progenies in large, pure single-progeny blocks, possibly outweighing the benefit of any genetic gain in being able to select 'crop' ideotypes, and (ii), in any case, the ideal tree type during a rotation may be one with the characteristics of both 'isolation' and 'crop' ideotypes, especially with repeated thinning. The condition for greatest genetic gain may be genotypes that are phenotypically 'plastic', or a mixture of genotypes differing in performance in isolation and competition. Larger and longer-term experiments are needed to further define the problem, to identify single-tree characters that are correlated with performance in competition, and to re-evaluate at least a few of the 'superior' genotypes that have been selected for seed production orchards in large pure blocks in the forest.

M. G. R. Cannell

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GENETIC GAIN BY CLONAL SELECTION OF SITKA SPRUCE AND LODGEPOLE PINE

During the last 10 years, many of the technical problems of rooting cuttings of *Picea sitchensis* and *Pinus contorta* have been solved, and there is now renewed interest in clonal forestry. The Forestry Commission (FC) is currently evaluating its first commercial conifer rooting facility, located near Elgin, and the Genetics Section of the FC Research Branch is seeking superior provenance and single-tree hybrids which can be propagated vegetatively. However, how large are the opportunities for genetic gain by clonal selection in *P. sitchensis* and *P. contorta*?

In 1972, ITE began an exploratory study to consider this question. Four clones were propagated from cuttings taken from 4 11/12-year old trees of each of 5 provenances of *P. sitchensis* and *P. contorta* growing in FC provenance trials. The provenances were chosen to span much of the range of each species (see legend to Figure 36), and the clone mother trees within provenances were chosen either at random (for *P. sitchensis*) or among trees of about average height within the provenances (for *P. contorta*). The rooted cuttings were planted in 1973/74 in replicated trials at both a lowland site (150 m altitude) on agricultural loams, and an upland site (310 m) in peaty-gley forest soils. In 1978, measurements were made of tree height, diameter, branching characteristics and phenology, and analyses were done to determine (i) the proportion of the total variation accounted for by provenances and clones within provenances, (ii) clonal heritabilities, and hence potential genetic gains by clonal selection in the test environments, and (iii) site x genotype interactions.

Clones within provenances accounted for 25–28% of the total variation in 5-year height in *P. sitchensis*, and 9–11% in *P. contorta* (Figure 36). The largest *P. sitchensis* clone within the smallest provenance (Cordova, Alaska, 60°N) was taller than the smallest clone within the largest provenance (North Bend, Oregon, 43°N). Similar variation existed in stem diameter (Cahalan 1981). There were visually striking differences among clones in branching and crown form characteristics (Figure 37, Plate 2). In both species, clones accounted for only slightly less of the total variation in branch number than provenances (eg 35% clonal and 38% provenance in *P. sitchensis*), but much more of the variation in branch angle (32% and 9% in *P. sitchensis*). Significant variation in the date of flushing and bud set were attributable equally to clones and provenances (Cahalan 1981).

Genetic analysis suggested that, by selecting the tallest 5% of *P. sitchensis* clones at the lowland site, a 73% gain in 5-year height could be expected, compared with the trial mean, which was approximately the value of the widely-grown Queen Charlotte Islands provenance. The equivalent genetic gain at the upland site was 53% (Table 31). Branch numbers in *P. sitchensis* could be more than doubled (or halved) by clonal selection; branch angle, length and straightness could all be changed greatly; the amount of late-summer lammas growth on *P. sitchensis* could be more than trebled; the date of flushing could be shifted by 10 days, and the date of bud set by 97 days (Table 31).

There were significant provenance x site and clone x site interactions for both species. In *P. sitchensis*, the relative heights of clones within 4 of the 5 provenances differed significantly between sites (Figure 36). Thus, considerable genetic gain could be obtained by selecting clones for specific sites.

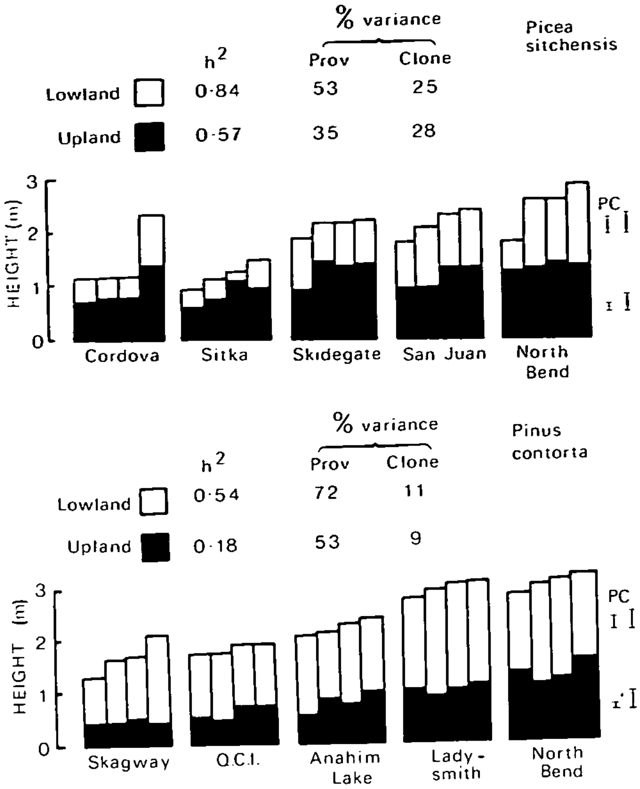

Figure 36 5-year heights of provenances and clones within provenances of Picea sitchensis *and* Pinus contorta *at an upland (shaded) and a lowland (unshaded) site in Scotland. The* P. sitchensis *provenances are: Cordova, Alaska (60°N); Sitka, Alaska (57°N); Skidegate, Queen Charlotte Islands (53°N); San Juan, Vancouver Island (49°N); and North Bend, Oregon (43°N). The* P. contorta *provenances are: Skagway, Alaska (59°N, < 150 m); Queen Charlotte Islands (54°N, 2150 m); Anahim Lake, British Columbia (52°N, 1220 m); Ladysmith, Vancouver Island (49°N, <150 m); and North Bend, Oregon (43°N, <150 m). The vertical bars on the right show the least significant differences (P = 0·05) between provenances (P) and clones (C), and values are shown of the clonal heritability (h²) and the contributions of clones and provenances to the total variance.*

It was unlikely that clonal heritabilities and expected genetic gains were overestimated because of 'c' effects – non-genetic effects arising from the fact that all ramets of one clone share the same environment on their mother tree – because (i) clonal differences in rootability were not correlated with subsequent performance, and (ii) there was no decrease in genetic variances with age (tree heights had been measured annually). However, to check this point, second-generation clonal trials were planted in 1980.

The genetic gains reported here are 3–7 times greater than those expected from first-generation seed orchards, but they can only be exploited on a large scale if large numbers of individuals can be propagated of individual genotypes. One of the obstacles to such propagation is that cuttings become increasingly difficult to root as the parent trees get larger and older. If this problem cannot be overcome, then the best method of capturing the large within-provenance variation demonstrated here may be to propagate vegetatively seedlings of single-tree controlled crosses that can be made year after year – an alternative being pursued by the Forestry Commission.

Clearly, the clonal variation demonstrated so far is only a tiny part of that which exists, and work is in progress to evaluate over 50 clones within a Queen Charlotte Islands provenance.

M. G. R. Cannell

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MANIPULATION OF CONE FORMATION IN THE CUPRESSACEAE

The family of coniferous trees which includes the cypresses, 'pencil cedars' and several other useful species of northern and southern hemispheres shares with the related redwoods (Taxodiaceae) the distinction of being the first group of forest trees in which sexual reproduction can be stimulated reliably (Hashizume 1973; Pharis & Kuo 1977; Longman *et al.* in press). Microgram or milligram doses of the plant hormone gibberellic acid (GA_3) induce the formation of many male and female cones in at least 35 species and hybrids in the Cupressaceae, and the response can be readily obtained in trees from 0·3 to 8 m or more in height, or alternatively just within a selected branch. Even seedlings in their first year can sometimes respond (Pharis 1975).

The ability to induce coning at will has far-reaching implications for forestry research and tree improvement. For instance, the changes which occur as the shoot apex switches from vegetative to reproductive activity can be monitored precisely, without having to climb tall trees or wait for uncertain seasons or years of cone production. Thus, in small *Thuja plicata* plants injected with 50 μg GA_3, both male and female cones were already beginning to develop after 4 weeks, and were at an advanced stage by 8 weeks (Plate 3a-f). Anatomical differences from vegetative apices were slight or non-apparent at 14 days, an observation which pinpoints the critical period when the change-over begins at the biochemical level.

Typically, female cones are formed on new wood towards the tips of branchlets, branches and trees, while male cones occur primarily on pre-existing, less vigorous, more proximal shoots. With a high dose of 500 μg GA_3 in a 0·3–0·5 m plant, most of the potential sites for cone formation will be occupied. Between the male and female zones, a few bisexual cones occur,

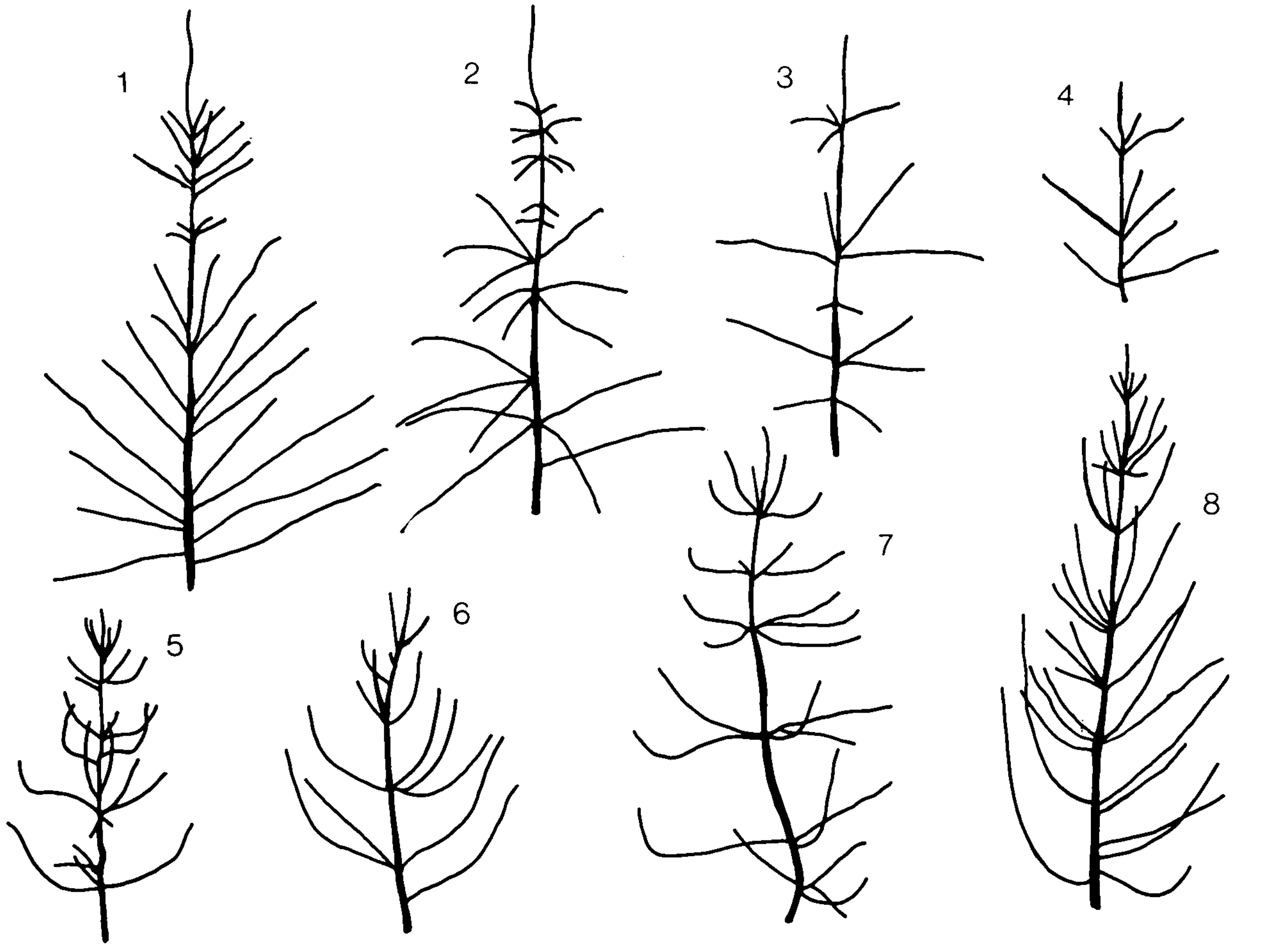

Figure 37 Line drawings from photographs of 4 clones of P. sitchensis *(1—4) and 4 clones of* P. contorta *(5—8) selected to illustrate the large differences in branching and crown form. 1 and 3 are clones of San Juan provenance, 2 and 4 Cordova, 5 and 6 Skagway, and 7 and 8 North Bend.*

Table 31. Mean, phenotypic standard deviation (σ_p), genetic gain (Δ G) and percentage gain over the mean, from clonal selection within *Picea sitchensis* and *Pinus contorta*. Gains were calculated from $\Delta G = i\, \sigma_p\, h^2$, where i is the intensity of selection, here taking a value of 2·06 (ie the top 5% of clones) and h^2 is the clonal heritability. *Days after 1st January.

	Character	Mean	σ P	Δ G	% gain
Picea sitchensis	Lowland site				
	Height (m)	2·03	0·86	1·49	73
	Diameter (cm)	3·80	1·45	2·27	60
	Branch number per tree	21·38	14·25	24·95	117
	Branch angle (°)	68·16	11·12	16·49	24
	Lammas growth (cm)	3·98	8·28	12·28	309
	Flushing date (days)*	140·06	6·92	10·83	8
	Date of bud set (days)*	243·30	55·88	97·16	40
	Upland site				
	Height (m)	1·06	0·48	0·57	53
	Diameter (cm)	2·17	1·02	1·05	48
Pinus contorta	Lowland site				
	Height (m)	2·24	0·47	0·52	23
	Diameter (cm)	5·21	1·44	1·48	28
	Branch number	8·18	3·93	2·51	31
	Branch angle (°)	55·20	17·28	16·73	30
	Whorl number	1·47	0·76	1·06	72
	Upland site				
	Height (m)	0·77	0·35	0·24	32
	Diameter (cm)	2·11	0·87	0·38	18

together with some 'neuter' apices which fail to complete the transition from the vegetative condition. Such a distribution suggests that there may be gradients of endogenous hormones or other substances within the shoot system which in some way determine sex. Alternatively, there may be a built-in predisposition to 'femaleness' or 'maleness' in the cellular organisation of the differing zones.

Applying a second growth substance into the same holes used to apply the GA_3 has been developed as a novel technique for screening a number of likely chemicals to see whether they have effects on levels of cone production, and/or sex distribution. Eight such growth substances were tested in 220 branches of 2 clones of *T. plicata*, 'chasing' a GA_3 dose of 50 µg, calculated to give moderately heavy male and female production. In the control branches (receiving only GA_3 plus solvents of the 'chasing' chemicals), clone 70 formed cones in 55% of apices, clone 139 in 40% (Figure 38). A high dose of 10 mg of 'Ethrel' (2-Chloroethanephosphoric acid, kindly provided by A. H. Marks & Company) depressed these levels to 47% and 27% respectively. The inhibition was most pronounced upon female cone production, so that the proportion of the GA_3-induced cones which were female dropped from 39% to 14% in clone 70, and from 14% to a very low 0·5% in clone 139. Observations suggested that the early stages of female cone initiation had often been reversed, indicating perhaps a genuine interaction between the ethylene liberated by the 'Ethrel' and the GA_3, rather than a toxic effect.

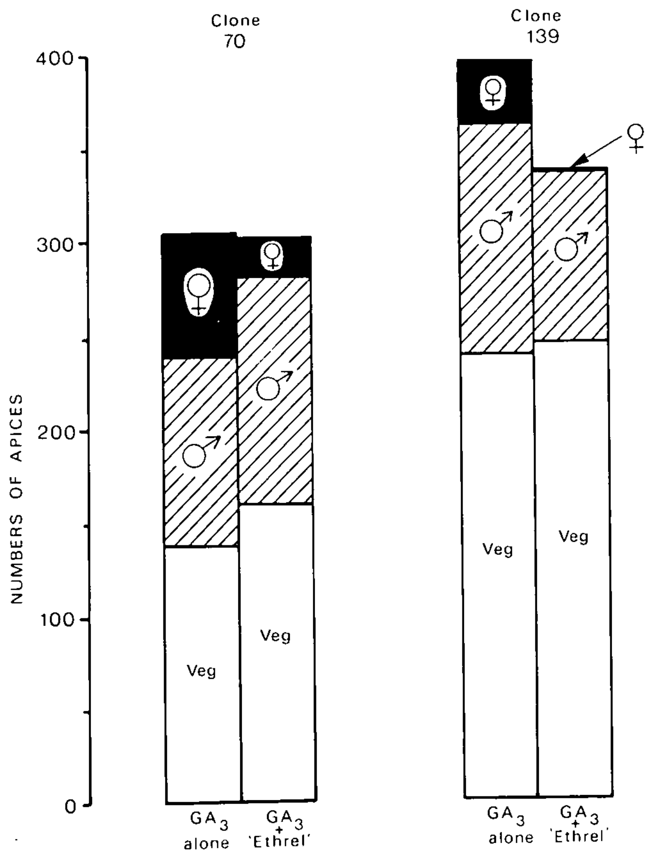

Figure 38 Clonal difference in response, and selective inhibitory effect of 'Ethrel' on female cone formation by gibberellin-treated branches in 2 clones of Thuja plicata.

Such a screening experiment allows chemicals influencing cone formation to be singled out for further study, where promotive as well as inhibitory concentrations may be discovered. A second growth substance, 'Alar' (succinic acid 2, 2-dimethyl hydrazide, kindly supplied by the Murphy Chemical Company), applied at 10 mg/branch, also had a somewhat inhibitory effect on the levels of cone initiation. However, here there was no significant alteration of sex ratio, but it was noticeable that cones could be detected at a very early stage. A second experiment demonstrated that both male and female cones were significantly larger when 'Alar' was given 5 or 10 days after GA_3, but not when its application was delayed to day 50.

Small GA_3-injected clonal plants of *T. plicata* have also been used in growth cabinet experiments to identify key environmental factors influencing cone formation (Longman & Edwards 1977; Longman 1981). At the same time, practical techniques have been developed to make large, widely-spaced trees in traditional seed orchards produce heavy crops of cones (Longman & Dick 1982). *T. plicata* is thus fulfilling its chosen role as a 'front-runner' for *Pinus contorta* (Longman 1982) and other more difficult forest tree species, where the control of reproduction is still largely a mystery. Moreover, its own status in Britain as a minor species could well be revised now that rapid breeding can be achieved, bringing a welcome addition of diversity to suitable sites. Its naturally durable heartwood makes it easy to understand why 10 times as much of its timber is cut on the west coast of the USA than that of *Picea sitchensis*, although there is more of the latter available.

K. A. Longman and R. Manurung

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THE GROWTH STRATEGY OF BRACKEN

Bracken (*Pteridium aquilinum*) is often regarded as a pernicious weed, although it has not always held this reputation; indeed, in the Middle Ages, it was regarded as a valuable crop. To the woollen and soap-making industries, it was a source of potash; to the farmer, it was bedding for his animals; and to the gardener, it was a valuable mulch. Regular collection of the fronds for all these purposes served to control the vigour and spread of the plant, but special features of its growth strategy have enabled it to take advantage of the degeneration of activities based on its cropping.

Dense stands of tall fronds may be produced on more fertile sites, giving standing crops with a dry weight in the order of 1200 g m^{-2}, which may be matched by a below-ground production of rhizomes exceeding 3000 g m^{-2} dry weight. This rhizome system not only produced the fronds, but is also responsible for the lateral extension of the plant, and is a storage organ in which starch is accumulated and used later to finance the early stages of growth before fronds have become fully functioning exporters of photosynthate.

How the rhizome system develops and reacts to different treatments are problems being investigated as part of a wider study of bracken aimed at finding effective means of control, or of using the species to provide a sustainable crop for energy production.

The bracken rhizome consists of a number of different components, as shown in Figure 39. The 2 basic units are the short shoot, which carries the fronds, and the long shoot which is frondless. (The terminology used here is that of Watt 1940.) Also present is a shoot of intermediate character, which may be seen to undergo transition from long to short shoot along its length, or *vice versa*. All 3 types of shoot carry buds, but they each develop differently.

Short shoots extend only slowly and produce fronds at close intervals, usually one per year from immediately behind the apex, giving the branch as a whole a zig-zag appearance. At the base of each frond is a bud which normally remains dormant, unless the frond itself is killed prior to normal autumn dieback, eg as a result of late frost or of cutting, when the basal bud will develop a replacement frond The length of time for which these buds are able to remain dormant is not known, but, in samples of rhizomes from the Forest of Dean, breaking buds have been found in positions on the short shoots which indicate that they have remained dormant for up to 12 years. This estimate is based on the assumption that a single frond has been produced each year by the length of short shoot examined.

Long shoots, which are frequently deeper within the soil, are thicker and are the main storage organs. They may attain considerable lengths, with buds or bifurcations separated by many centimetres. They carry no fronds.

Intermediate shoots have characteristics of both long and short shoots, though the extent to which they resemble either type may vary along a single branch. Like the long shoots, they may grow to considerable lengths and branch at long, irregular intervals, but, like the short shoots, they carry fronds, though production of these may not be restricted to one per year. In pot cultures established from sections of mature systems, there is a large production and extensive growth of intermediate rhizome during the first growing season, followed by a more distinct differentiation into long and short shoots in subsequent seasons.

Newly-established pot cultures show certain differences from the field situation, mainly as a result of the lack of balance between apical regions and older parts of the system. These pot cultures represent rejuvenated sections of rhizome and, as such, care must be taken, particularly in the early stages of growth, in relating any results back to field conditions. Experiments with rhizome lengths in pots do, however, give some indications of the plant's reaction to certain forms of treatment.

Different types of rhizome segment behave in much the same way in pot culture. Lengths of short or long shoot, or segments containing both types, rapidly produce several fronds from any buds already present, and produce long intermediate shoots which themselves also produce new fronds during the growing season. However, a high degree of variability is found between the production of rhizome and fronds, even within samples of the same initial rhizome type. For example, the maximum and minimum values for length of new rhizome produced (398 cm and 27 cm) in experimental transplants of rhizome segments were both from equal lengths of short shoot. Overall means were 115·6 cm of new rhizome carrying 21·9 buds and with 20 expanded or developing fronds, from an original 24 cm segment carrying 4 buds. Continued growth of the new intermediate rhizome and its fronds is dependent upon the fronds already present, either on the original segment or produced during the earliest part of the season on the new rhizome. If these fronds are removed, more of the rhizome reserves are diverted into the production of new fronds, which tend to be progressively smaller. A similar reduction in frond vigour may be seen in the field, where cutting has taken place. A single cut at the end of May reduces the mean height of fronds, and also their density. A further cut in July, which removes the new crop of replacement fronds, produces an even greater reduction in height and density of the following crop. Mid-September values for the Forest of Dean site are as follows:

	Frond density	Frond height
Uncut	40 ± 10·4 fronds m^{-2}	183 ± 22 cm
1 Cut	26 ± 2·2 fronds m^{-2}	128 ± 15 cm
2 Cut	10·6 ± 7·4 fronds m^{-2}	67 ± 4 cm

No significant difference was detected in the weights of rhizome at the end of the first growing season, although the number of buds present on the rhizome did increase from 268 m^{-2} in the control plots to 546 m^{-2} in the twice-cut plots.

It is hoped that continuation of the field trials will indicate the extent to which modification of the growth pattern of the rhizome varies in response to continued treatment and the possible reversion following cessation of cutting. In parallel with these field investigations, further observations will be made on the development of more mature rhizome systems in pot culture and on the partitioning of resources, not only between the fronds and rhizomes, but also between different components of the rhizome system itself.

R. E. Daniels

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POPULATION ECOLOGY OF THE MARSH GENTIAN *(GENTIANA PNEUMONANTHE)*

Experimental studies and observation of natural populations of the marsh gentian (*Gentiana pneumonanthe*) have shown a wide range of performance by this plant in terms of both vegetative growth, flowering and seed production (Plate 9). A number of factors have been found to affect performance, and these include soil temperature, air temperature, and nutrition. However, the most dramatic effect that has been observed is the reduction in flower, and therefore seed, production that occurs when the gentian plant is growing in association with a number of other heathland plants, especially *Calluna* or *Erica tetralix*. Several pot experiments are in progress that have been designed to investigate this effect of competition upon the marsh gentian. At present, it seems most likely that the effect is one of competition for nutrients, and that, under natural conditions, the plant is growing in situations far from optimum for maximum performance in terms of either vegetative or sexual growth.

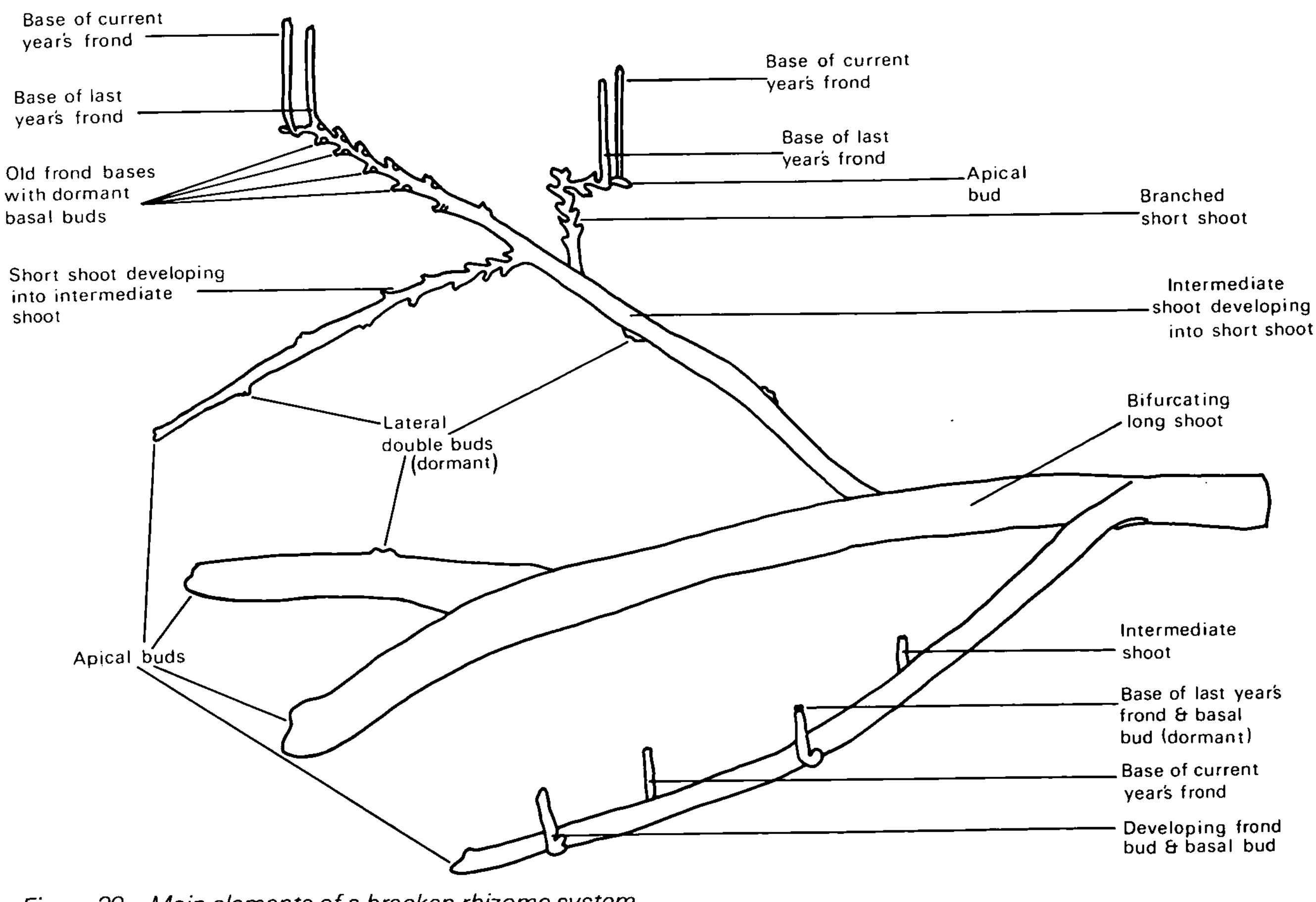

Figure 39 Main elements of a bracken rhizome system.

Observations from a number of field populations have provided initial estimates of population levels, performance, recruitment and mortality under natural conditions, and these data have been incorporated in a computer model that can be used to simulate and investigate the possible performance of *Gentiana* populations in competition with associated heathland vegetation.

The model makes the basic assumption that, as the standing crop of the heather vegetation increases with age, then the flowering performance of the gentian plants is reduced. In the absence of heather burning, the simulated *Gentiana* population becomes extinct after about 40 years. Different burning regimes have been simulated by the model and suggest that an oscillating, but otherwise steady, population of gentians will be maintained with burning every 13 years. A further development allows variation to be introduced into the model parameters so that annual variation can be considered, and further runs provide output on the mean performance of the population, along with the confidence limits for the model (Figure 40). These limits represent the range within which any single run of the model might be expected to fall 90% or 95% of the time.

Investigations into the stability and performance of the model suggest that it provides a reasonable description of natural populations of *Gentiana pneumonanthe*, and that survival of the plant depends upon longevity combined with periodic suppression of competition by fire or grazing. Shortcomings in the present model are that it ignores the effect of pattern in the community which develops after a series of heathland fires. However, the construction of such population models develops a better understanding of the processes involved, and generates several hypotheses relating to the natural populations that can be tested.

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THE USE OF ISOENZYMES IN THE ANALYSIS OF PLANT POPULATION STRUCTURE

The detection of variation at many gene loci within a single individual, which has become possible since the advent of electrophoresis, has not only revolutionised population genetics, but has had many side effects. One of these is the contribution which isoenzyme polymorphisms have made to analysis of the spatial structure of plant populations. Two types of analysis may be distinguished. In the first, the prime objective is to detect the number and size of individuals (genets) in a clonally-spreading morphologically-uniform species, often in almost pure swards. In the second, where the number and size of individuals is usually known, the principal interest is in the spatial distribution of alleles or genotypes.

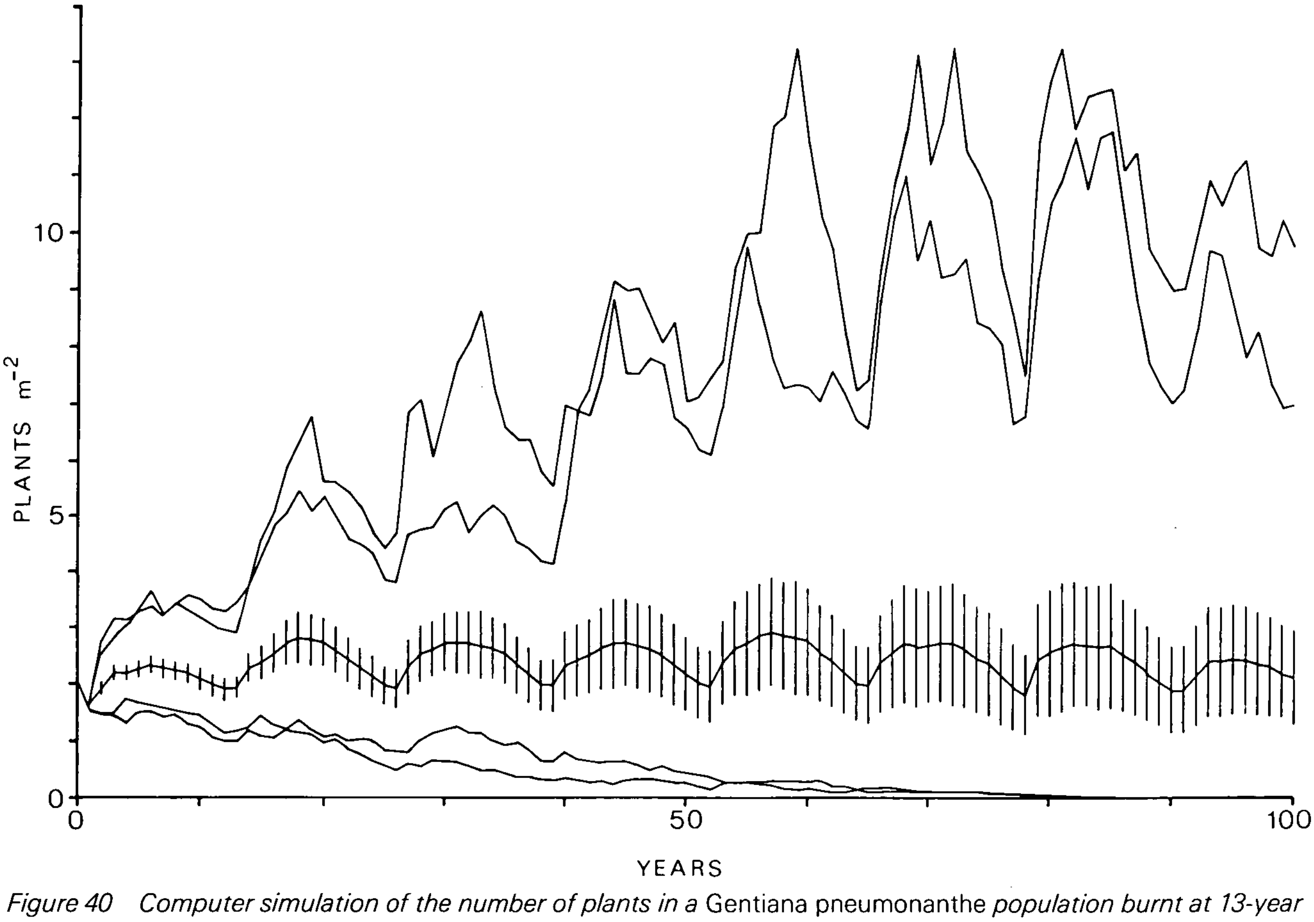

Figure 40 Computer simulation of the number of plants in a Gentiana pneumonanthe *population burnt at 13-year intervals. Central plot represents the mean response of the model (with 95% confidence limits of the mean). Outer plots represent limits within which 90% and 95% of single runs should fall.*

Studies of clonal structure in natural populations of sward-forming species were pioneered by Harberd (eg 1961, 1962, 1967), who used mainly morphological and incompatibility characters to delineate individual plants. He showed that some natural populations of, for example, *Festuca ovina* and *Holcus mollis* may become dominated by a single, very large, old clone, or very few clones – results which contrast with many recent studies, eg Burdon (1980) on *Trifolium repens*, which have demonstrated the presence of many, varied clones in a relatively small area. The first use of isoenzyme variation in clonal analysis was probably that of Wu *et al.* (1975), working on copper-tolerant populations of *Agrostis stolonifera*. Variation in esterase enzyme, of unknown genetic control, was matched to morphological variation and copper tolerance in 30 tillers taken at 20 cm intervals on a transect across a lawn. The first analysis of individual clone sizes using a grid sampling system was that of Gray *et al.* (1979), although, clearly, Silander (1979) had used a similar method independently and simultaneously in North America. Interestingly, both the species involved were salt marsh grasses. Gray *et al.* (1979), using 25 cm grid intervals and 9 polymorphic loci in 3 enzyme systems, demonstrated that a grazed population of *Puccinellia maritima* contained fewer, larger clones per unit area than a nearby ungrazed population. Silander, using 14 polymorphisms and a 1 m grid, revealed a similar contrast in clone size and number between natural populations of *Spartina patens* from dune, slack and salt marsh habitats.

A grid method has recently been applied to sown pasture areas by Roose and McNeilly (pers. comm.) to compare clone structure in *Lolium perenne* swards of different age and under different management regimes. Changes in genotypic frequencies in ryegrass swards have been studied by Hayward *et al.* (1978), using isoenzyme variation.

The study of spatial distribution of genetic variation in plant populations has a long history, although spatial variation in isoenzyme polymorphisms has only been investigated relatively recently, mainly in North America by Allard and his associates (eg Hamrick & Allard 1972) working on wild oat (*Avena*) species. The most complete analysis of spatial variation in gene frequencies allied to ecological and demographic variables is that of Schaal, whose seminal work on the prairie herb (*Liatris cylindracea*) demonstrated significant heterogeneity of gene frequencies between adjacent 3 m^2 quadrats (Schaal 1975; Schaal & Levin 1976). This very marked substructuring of the population was attributed to restricted gene flow, caused largely by pollinator behaviour, and could not be related to environmental (edaphic) variation.

This result contrasts with those recently obtained for variation at several isoenzyme loci in a post-fire population of *Agrostis setacea* (ITE 649). Following a fire in 1976 which destroyed the existing heathland vegetation over much of Hartland Moor, Dorset, colonization by *A. setacea* has been studied – the birth, flowering performance and death of all individuals in a permanent quadrat (40 m^2 total area) on sloping ground being mapped annually. Leaves were taken from those individuals large enough to sample, mainly 1976 and 1977 recruits, and variation in 7 enzyme systems known to have polymorphic loci were examined by starch gel electrophoresis. Variation at 2 loci, Esterase (Est) 2 and Glutamate oxaloacetate transaminase (Got) 3, is shown in Figure 41. Variation at both loci is known from breeding experiments to be under genetic control, with 2 alleles at Est 2 and 3 alleles at Got 3. The most interesting feature of the variation pattern is the increase in frequency of Est 2a and the decrease in frequency of Got 3c towards the bottom of the slope (the right-hand side of the diagram). The significant differences between the 2 halves of the quadrat in allele frequency are typical of variation in 8 out of 9 loci examined, and variation in 5 of these corresponds exactly with a regional east/west population cline. Alleles such as Est 2a, which increase in frequency in natural populations in a westerly direction in south-west Britain (from a mean of 0·28 in Surrey to 0·44 in south Wales), also increase in frequency at the bottom, presumably wetter, part of the slope. Got 3c is typical of those alleles increasing in an easterly direction (from 0·12 in west Cornwall to 0·20 in Surrey), which also have a higher frequency at the top of the slope on the Hartland quadrats. This correspondence between regional and local distribution

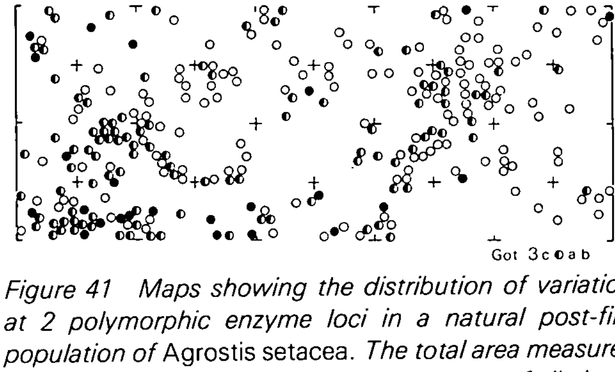

Figure 41 Maps showing the distribution of variation at 2 polymorphic enzyme loci in a natural post-fire population of Agrostis setacea. *The total area measures 4 × 10 m, and the maps show the genotype of all plants large enough to sample without affecting future growth. (a) Esterase 2: ● homozygote aa; ○ homozygote bb; ◐ heterozygote ab. (b) Glutomate oxaloacetate transaminase 3: ● homozygote cc; ○ either aa, ab or bb; ○ heterozygote ac or bc. (Got heterozygotes are 3-banded indicating a dimeric enzyme)*

implies that rainfall or soil moisture, or some aspect of soil water balance, is a selective force producing variation in population genetic structure in *A. setacea*, a possibility being investigated by further genetic and demographic studies, and by experiment.

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Plant Community Ecology

THE EFFECTS OF TREE SPECIES, PLANTED PURE AND IN MIXTURES, ON VEGETATION AND SOIL AT GISBURN

In what way do different species of trees influence the site on which they are planted? Do mixed tree stands have advantages over monocultures? The experiment at Gisburn, planted in 1955 on a site originally uniform, seeks to answer such questions. Earlier reports emphasised differences between the pure species stands (Brown 1978; Howson & Brown 1980), and this report describes current work to elucidate mixture effects.

The layout of the 6 mixed plots (containing groups of 18 trees of one species alternating in each direction with similar groups of the admixed species) allows soil and vegetation beneath a given canopy species to be studied, either when influenced by various admixed tree species, or without such influence in the 4 pure stands. These tree canopy combinations are shown in Table 32.

An intensive survey of the vegetation in one of the 3 replicates was carried out in the summer of 1980, together with a measure of light intensity at each of the 1100 quadrat positions. Differences in percentage frequency and representation of selected species under the different canopies are shown in Table 32. The results indicate that:

1. Certain ground flora species are associated with particular trees (whether mixed or pure).
   i. Significantly associated with alder (*Alnus glutinosa*) are *Agrostis tenuis*, *Deschampsia cespitosa*, *Galium saxatile*, *Eurhynchium praelongum*, *Lophocolea bidentata/cuspidata* and *Rhytidiadelphus squarrosus*.
   ii. Oak (*Quercus petraea*) contains significantly higher frequencies of *Dicranella heteromalla* and *Polytrichum* spp.
   iii. Norway spruce (*Picea abies*), although in general containing few species with low frequencies, has *Calypogeia* spp, *Mnium hornum* and *Lepidozia* spp associated particularly or solely with it.
2. There are some clear mixture interactions.
   i. The effect of Scots pine (*Pinus sylvestris*) in mixture is especially marked, significantly altering the frequency of several ground flora species under the canopies of trees with which it is mixed. *A. tenuis, D. cespitosa* and *E. praelongum* all increase under oak and alder when pine is present, but the frequency of *Carex nigra*, *Deschampsia flexuosa* and *Polytrichum* spp is greatly reduced under both of these mixed canopies.
   ii. *Vaccinium myrtillus* is present under pine, oak and alder only when Norway spruce is also present. Similarly, the strict calcifuge *D. flexuosa* is at its maximum frequency in such mixtures. Mixing with spruce also significantly increases the frequencies of *Hypnum cupressiforme* under oak and alder, but reduces *Galium saxatile* under pine.

Although low light intensity (also shown in Table 32) may account for much of the considerable reduction in representation or frequency of species under spruce, light does not appear to account for many of the other differences in vegetation. It seems more likely that soil differences, now developing in the different tree plots, are important in determining the present ground flora. Knowledge of the ecology of the above groups of species suggests that the soil under oak is base-poor and acid, whereas alder appears to have an appreciably more fertile soil, with some tendency towards becoming a mull (indicated especially by *D. cespitosa*). From its marked effect on the vegetation under trees with which it is planted, pine at Gisburn is evidently a soil improver when in mixture. In contrast, alder, despite the better soils it seems to produce under its own canopy, has no obvious influence on vegetation under other trees with which it is mixed. Spruce in mixture appears to lead to some impoverishment of the site.

Table 32. Percentage frequency of selected ground flora species under different tree canopies (pure and mixed): Gisburn, 1980

Canopy	Scots pine (SP)				Norway spruce (NS)				Oak (OK)				Alder (AL)			
Admixed species	SP*	NS	OK	AL	SP	NS*	OK	AL	SP	NS	OK*	AL	SP	NS	OK	AL*
Agrostis tenuis			9	17					16				65	11	4	6
Carex nigra	4		3	2			4	4	3	56	65	62		27	59	77
Deschampsia cespitosa			5	6					7				18	3	1	3
Deschampsia flexuosa	51	51	33	30	8	1	40	25	44	98	61	89	29	98	91	86
Festuca ovina/rubra			2	1					3	1	16	3		2	3	22
Galium saxatile	58	19	43	53	9			1	44	16	7	28	80	83	90	95
Juncus effusus										2	2	3	1	2	8	
Nardus stricta							1			12	2			2		4
Potentilla erecta										4				2		1
Vaccinium myrtillus		4					1			2				7		
Calypogeia spp						3	9									
Dicranella heteromalla	1	1	1	3	1	1	7	1	4	10	16	7		1		8
Dicranum scoparium						1	2			5	7					
Eurhynchium praelongum			4						13		3		23	11	2	2
Hypnum cupressiforme	5	11	4	4	9	18	34	27	18	53	19	35	15	69	28	28
Isopterygium elegans							4				1					
Lophocolea bidentata/ cuspidata	9	13	18	15	4	5	7	12	31	47	13	36	69	79	60	60
Mnium hornum		1			1	2	5	3	1		1	1	1	1		
Plagiothecium undulatum		4			1	3	3		2	3			2	4		
Pohlia nutans	1	1			2	3	23			19	28	4			2	8
Polytrichum commune/ formosum							9	3	9	36	60	46	9	27	23	22
Rhytidiadelphus squarrosus									1	1			14	8	1	2
Lepidozia spp						1	2									
Bare ground	20	34	31	23	75	73	31	62	13							
Average light intensity (% of open)	8	4	5	8	3	1	2	1	5	10	10	4	10	18	10	11

Frequencies underlined are those significantly different from others within (single lines) or between (double lines) canopy types.
*The pure stands of these species

Further analysis of the 1980 data, using ordination, confirms that differences in light intensity explain at most only about 30% of the variation in species composition (much of which is the difference between spruce and non-spruce); soil differences appear to be at least as important, with pH alone accounting for a similar proportion of the variation. Based on data available from the monoculture stands, there are indications that soil phosphorus levels are also important in influencing floristics. Studies reported elsewhere in this report (Harrison *et al.*, pp. 84 – 85) confirm that soil phosphorus is a key factor on this site, and that pine is clearly superior to alder as an admixed species, as far as improving the growth and phosphorus status of spruce is concerned.

A. H. F. Brown

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MONITORING IN WOODLANDS

(This work was largely supported by Nature Conservancy Council funds)

Descriptions of vegetation are sometimes based only on lists of species present, recorded either in a series of quadrats or by some less formal method. More often, however, a quantitative estimate is made of the contribution of different species, which may help in interpretation when it is necessary to recognise changing balance between species. The quickest method is to make a visual estimate of the canopy coverage, or cover, of different species in a quadrat.

In situations where large quantities of data have to be collected by different people, or where sequential data are to be compared to see whether changes have occurred, it is important to know the size of the smallest cover interval which can be distinguished reliably. In both situations, errors may result either from:

i. the inability of an observer to produce a consistent estimate on 2 or more occasions; or
ii. the inconsistency between different observers on one or more occasions.

The size of these errors has been examined in a series of quadrats in Roudsea Wood NNR by 10 observers making repeated cover estimates of species occurring in the quadrats during summer.

Significant differences occurred between observers' estimates for most species. Variability between observers was usually lowest when estimating broad-leaved species such as *Mercurialis perennis* and *Vaccinium myrtillus*, and highest for fine-leaved species such as grasses, and for bryophytes. An observer drawn at random from the group would be expected, in most circumstances, to return an estimate within 10-20% of the group mean; the same observer would be expected to repeat an estimate on the same quadrat within 5–15%.

There was a clear tendency for individual observers to estimate lower or higher than the group, although they differed in the consistency of their bias both within and between species. It is, therefore, possible, and will sometimes be worthwhile, to calibrate observers against a standard so as to reduce the effect of their bias.

J. M. Sykes and A. D. Horrill

MAPPING BROADLAND VEGETATION

The Broadland area of Norfolk and Suffolk, comprising the flood plains of 4 major rivers, is characterised by a mosaic of open water, reed beds, marshland and wet woodlands called carrs. The flood plains have been used by man for centuries to provide reeds for thatching, and grazing land for cattle; medieval peat excavations have created freshwater lakes called Broads. Traditional management is declining, amenity use has greatly increased, intensive arable farming threatens much of the former grazing marshes, and nutrient enrichment has seriously affected the water quality. The natural invasion of open water by reed-swamp, a key stage in the succession to fens and carrs, has turned to widespread recession (Boorman *et al.* 1979), with introduced grazing animals, and especially coypu, being mainly to blame (Boorman & Fuller 1981).

In order to monitor the changing ecology of Broadland, 300 km^2 of flood plain are being mapped. Sixteen types of semi-natural vegetation, plus 15 land use categories, have been interpreted from 1:10000 black-and-white photographs. Details have been transferred on to existing topographic maps at the 1:10000 scale, using a Bausch and Lomb Stereo Zoom Transfer Scope. By means of zoom and stretch controls on the instrument, the photographic scale may be matched to that of the map to achieve an accurate plot, despite tilts and scale variation between photographs. A series of 1:1000 colour transparencies has been taken as a stratified random sample of 'quadrats' for verifying the interpretations made using the 1:10000 prints. A small part of the area will be surveyed using photogrammetric plotting techniques to assess the accuracy of the transfer methods.

The vegetation and land use outlines are being digitised on to a computer at the NERC Experimental Cartography Unit (Fuller & Drummond 1981). An electronic cursor is traced manually along the lines, which it records as a series of x and y co-ordinates. The data are then used to print high-quality output maps on a light projection plotter, at the 1:10000 scale, shaded as appropriate, and to calculate the areas of land parcels, and lengths of linear features such as rivers, ditches and roads.

The maps and data will form a baseline against which future changes can be measured; they can then be updated as necessary by new photo-interpretation and subsequent interactive editing of the original data base. The information will be used to examine how the distribution of plant communities is influenced by environmental factors such as water quality, soil type, topography and land use.

R. M. Fuller

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RECOVERY OF VEGETATION IN A CALEDONIAN PINEWOOD AFTER FIRE

(This work was largely supported by Nature Conservancy Council funds)

Following a wildfire in the Caledonian pinewood at Shieldaig, Wester Ross, in late March 1974, the recovery of the vegetation, particularly Scots pine (*Pinus sylvestris*) seedlings, was monitored in 20 sample plots. Almost all trees under 5 cm diameter at breast height were immediately killed by the fire and, of the large trees in the sample plots, 45% of the Scots pine and 60% of the birch (*Betula pendula*) had died by 1980 (Plate 10). In addition to the primary effects of the fire, secondary effects resulted from the activity of the pine shoot beetle (*Tomicus piniperda*) which caused damage to trees whose vigour had been reduced by the fire.

Birch seedlings were completely eliminated from the plots by the fire but 95% of them contained birch seedlings by 1980. During the 2 months between the fire and the first survey, pine seeds, presumably shed after the fire, had germinated in 11 of the 20 sample plots, with a mean number of 2·3 seedlings per plot, equivalent to approximately 950 ha^{-1}. Many more appeared later in 1974 and the mean number rose to 4·9 (2000 ha^{-1}) by 1975. Additional seedlings were recorded every year except 1980 but had been offset by deaths, so that seedling density has remained about 2500 ha^{-1} since 1977. Mortality was heavy during the early stages of establishment and almost 40% of the seedlings were classed as unhealthy in 1980, many of them growing in shade, on pine litter, or on shallow peat.

Changes in frequency of occurrence of field layer plant species recorded between 1974 and 1980 suggested 2 main types of recovery from the fire. Species with constant frequency tended either to occur in wet habitats where the fire was less intense, eg *Narthecium ossifragum*, *Pedicularis sylvatica*, *Carex echinata*, or to have robust rhizomes or rootstocks, eg *Blechnum spicant*, *Pteridium aquilinum* and *Molinia caerulea*. Cover values for the last 2 species increased during the 1975 growing season but subsequently declined, suggesting that the fire may have temporarily stimulated growth. Species with less persistent underground organs survived the fire less well in most areas. Regrowth was largely from unburned remnants and from buried or imported seed. Species in this category tended to increase in frequency and in cover, eg *Galium saxatile*, *Calluna vulgaris*, *Erica cinerea* and a number of grasses. *Calluna* regenerated from stem bases only on wet ground, where it occurred sparsely; elsewhere it was tall and straggly and did not survive. However, it regenerated easily from seed, and a significant increase in mean cover value continued until 1980. An estimate of the charred mats of pleurocarpous mosses in 1974 suggested a mean cover of at least 30% before the fire, whereas there was less than 5% afterwards. Bryophyte recovery followed the same course as that of *Calluna*, with regeneration probably coming both from spores and small surviving fragments. Re-establishment of pleurocarpous mosses such as *Hylocomium splendens* and *Pleurozium schreberi*, which seldom produce spores, was largely from remnants, often badly scorched, which survived in crevices and beneath rocks.

The obvious manifestations of fire had largely disappeared by 1980, but a few dead pine saplings and some bare rock surfaces remained. Changes in species composition and abundance were still occurring, though structural changes, such as the death of pine saplings and mature *Calluna* plants, were the most obvious results of the fire. Changes in the balance between *Calluna* and *Pteridium* on drier sites may have important implications for the regeneration of pine in some parts of the wood.

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SCRUB CONTROL ON LOWLAND HEATHS

(This work was largely supported by Nature Conservancy Council funds)

On many heaths in lowland England, where there is now little or no management, succession to scrub woodland is occurring. In particular, birch, pine and bracken are invading these areas, and active control of these 'weed' species is essential if an open heathland habitat is to be maintained. Whilst research on all these species is in progress in ITE, this report concentrates on the control of birch scrub.

As birch regenerates rapidly after mechanical treatments such as cutting, a herbicide-based control strategy is required for the efficient control of this species. There are 3 main strategies that may be used:

i. spraying trees with herbicides; this produces the 'graveyard' effect (Plate 11), and is clearly unacceptable from an aesthetic viewpoint, unless followed by a cutting treatment;
ii. spraying the regrowth produced after cutting with herbicides;
iii. applying herbicides to cut stumps.

There are, however, constraints to the use of herbicides on nature reserves; for example, selective herbicides should be used in both the first 2 strategies in order to minimise damage to desirable species, and control will be entirely dependent on the selectivity of the herbicide. Alternatively, non-selective herbicides could be used, if selectivity can be achieved through the method of application, for example in the third strategy where local application of herbicide reduces the risk of damage to non-target species. Ideally, the best strategy for nature conservation would be the local application of a selective herbicide.

Two herbicides, ammonium sulphamate and 2,4,5-T, are currently recommended for scrub control (Fryer & Makepeace 1978). Ammonium sulphamate is a non-selective herbicide and is usually applied to cut stumps; it is unlikely to be used in a foliar spray in sensitive conservation areas. 2,4,5-T, on the other hand, is a selective herbicide, active against woody species, and can be applied either to foliage in a spray or to cut stumps. Since 1978, there has been a dramatic reduction in the use of 2,4,5-T because of public concern about its safety, which has depleted the techniques available for controlling scrub in nature reserves.

Several herbicides have been developed recently which may prove useful for the control of birch on lowland heaths, and include selective herbicides, like krenite and trichlopyr, and also hexazinone, tebuthiuron and the agricultural herbicide glyphosate. Experiments have been set up to investigate the effectiveness of the selective herbicides when applied to birch as a foliar spray, and of applying all herbicides to cut stumps. In addition, typical grass and *Calluna* heaths have been sprayed at the recommended rates to investigate the effects on non-target species.

It is hoped that these experiments will provide a framework for birch control programmes on lowland heaths for conservation purposes.

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GRAZING STUDIES ON SAND DUNES

The large reduction in the rabbit population in Britain in the mid-1950s and the subsequent changes in vegetation have been recorded extensively (Thomas 1960, 1963; Ranwell 1960). The previously short, species-rich, turf, with many annuals, gradually changed to tall grass and tall herb communities. Subsequent invasion by shrubs gave rise to vegetation consisting mainly of woody species, accompanied by lowered species diversity. Nature conservationists became concerned about the changes and the possible loss of species. Experiments to study management of chalk downs and fens were started (Wells 1971; Williams *et al.* 1974), but information on sand dune communities was lacking. On the one hand, it was thought necessary to reduce the tall communities to short ones in order to increase 'species diversity', and, on the other hand, there was concern that some dunes were being over-grazed, leading to erosion, eg the Bornish blow-out (Seaton 1968).

An experiment was designed to investigate:

i. the floristic consequence of introducing known levels of grazing on previously ungrazed swards;
ii. the differential effects of seasonal grazing and the number of animals per unit area on the flora;
iii. the requirements, in terms of animals and time of year, for producing swards of particular floristic compositions.

With the co-operation of the North Wales Region of the Nature Conservancy Council, an area of 24 acres (9·7 ha) was fenced at Newborough Warren – Ynys Llanddwyn NNR, Anglesey, Gwynedd. This area of dune hinterland has been divided into 2 blocks, each of 16 ¾-acre (0·3 ha) paddocks. The various treatments were allocated randomly to the paddocks and are replicated in each block. The topography ranges from low dunes to wet slack, which usually floods for part of the winter. From a preliminary survey, an indicator species analysis of the data produced 6 vegetation types. On the dunes, above the influence of the water-table, 2 tall grass vegetation types occur, one with *Arrhenatherum elatius* and the other with *Ammophila arenaria*. Also on the dunes is a similar fixed dune type, but without *Ammophila*. In the slacks, where the water-table is the over-riding influence, the 3 vegetation types recognised range from dry through damp to wet. At the dry end of the scale, species such as *Festuca ovina*, *F. rubra* and *Carex arenaria* are important, while, at the wet end of the range, *Mentha aquatica*, *Hydrocotyle vulgaris* and *Carex nigra* are present. There are no distinct breaks in the variation between these vegetation types. While this amount of variation in the experimental area is not ideal when interpreting the experimental results, information on the reaction over this range of vegetation types is needed, if one is to predict the effects of grazing on dune pastures in general.

Originally, interest in the effects of grazing animals on vegetation in the dune system arose from a study of ponies and rabbits on dunes in south Wales. It was not practicable to obtain the number of ponies needed, but it was possible to use Soay sheep. These animals have the advantage of being unlikely to be stolen, as might be the case with a domestic breed, and they are light to handle. They do have the disadvantages of being extremely agile and rather shy, but, with careful handling, they become quite tame. In other respects, they require looking after in the same way as other sheep breeds, eg dipping is a statutory requirement.

There are 2 intensities of grazing in the experiment, with stocking density being the equivalent of either one sheep or 2 sheep per plot, with flocks of 4 and 8 sheep in each block to allow for the natural flocking instincts of the animals. In practice, the animals are moved to a new plot each week, assuming that one sheep for 4 weeks has the same effect as 4 sheep for one week. For most of the year, the assumption is reasonable, but, during peak growth in June, the vegetation is grazed at slightly different phases at the time of its maximum development. There are advantages in this system in that rarer plant species have a greater chance of flowering and setting seed, and the pastures are rested, which should reduce the rate of increase in animal parasite numbers. To investigate the effect of grazing at different times of year, the year is divided into thirds, namely January-April, May-August, and September-December. The complete combination of one third, 2 thirds, and whole year grazing periods is included in the experiment. There are also 2 ungrazed plots in each block as controls.

So far, the most visually obvious effects have occurred in the plots with the larger number of sheep. An interesting example is shown by *Arrhenatherum elatius*. Plate 12a shows the boundary between an ungrazed plot and the most heavily grazed one, taken in July 1981. The small mounds are the remains of *Arrhenatherum* tussocks which are now beginning to break up and become detached from the soil. In the early stages of grazing the tussocks, the sheep open them in winter to eat the swollen stem bases. Plates 12b and c show the state of decay after 3 grazing seasons. Although tussocks are dead, *Arrhenatherum* is still present in the sward which developed as a result of sheep grazing, but *Salix repens*, *Crataegus monogyna*, and *Betula* sp have been affected adversely (Plate 12d). The sheep are able to remove the buds skilfully as they flush in spring, killing the young shoots. In addition, the tree trunks are de-barked and frayed in the autumn and winter. *Prunus spinosa* has not been affected seriously, but it is not known if this is because of the unpalatability of the foliage or the spines on the stems. The dune ridges are attractive to the animals for 'camping', which has resulted in damage to the turf where the sheep lay, and clear effects of dunging and urine are visible. On the level, camping grounds are not clearly defined and the patches of dung are more widely spread. The damage to the turf could cause blow-outs, but it may also allow annuals to invade if seeds are available. Both densities of animals are having discernible effects on the vegetation, but the changes have not yet produced a flora comparable with some of the grazed dune systems elsewhere in Britain.

D. G. Hewett

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SOME CURRENT PROBLEMS OF SEA COAST VEGETATION MANAGEMENT

The sea coast is an unstable boundary between the sea and the land. Vegetation can aid sea defence against tidal flooding by reducing wave action, and assists coastal protection by reducing erosion, but only within certain limits. Ecological advice is needed to determine these limits, which species should be used, how and when they should be planted, and in what ways coastal vegetation should be managed.

Hard engineering structures are essential in coastal protection where wave energies are high. However, these structures are increasingly expensive to erect and maintain, and there are many areas where lighter engineering structures can be used in conjunction with vegetation to control erosion at relatively low cost. For example, stone-filled, wire mesh gabions were used to control toe erosion of dunes at Pilmour Links, Fife, and the steep sand above them was successfully stabilized with mixed plantings of marram (*Ammophila arenaria*) and sea lyme grass (*Elmus arenarius*). At Camber, Sussex, chestnut pale fencing was used to check sand drift and raise dunes to levels where marram plantings could survive. Large areas of bare sand were successfully stabilized at this site with hydraulically-seeded, commercial grass strains.

Immature sediments are often low in humus and nutrients and the securing of graded soft coast cliffs at Highcliffe, Dorset, was only achieved by seeding on to a surface mulch of soil to which fertilizers had been added (Gray *et al.* 1981).

In contrast to the low nutrient situation at Highcliffe, excess nutrients, believed to derive from sewage effluent and fertilizer outwash, can also create problems, for example in southern harbours such as Langstone Harbour, Hampshire. High nutrient levels favour excess algal growth which aggravates oxygen depletion in salt marsh soils that may already be waterlogged by land subsidence. One solution seems to lie in using dredge spoil to restore levels for healthy salt marsh growth. Brushwood enclosures on mud-flats at Dengie, Essex, are being used to encourage sedimentation, and aeration is improved by a specially cut system of drainage ditches. Advice has been given to the Anglian Water Authority on the establishment of salt marsh plants within the sedimentation fields.

Plants are not always desirable. For example, problems have arisen in the Ribble Estuary, Merseyside, as a result of salt marsh (*Spartina*) invasion near the holiday resort of Southport. Plant growth has been checked successfully by aerial spraying with herbicides which are harmless to the invertebrates on which birds feed. In the long term, salt marsh inevitably leads to reclamation, and advice has recently been given to the Merseyside County Council on the wildlife resources and management of newly reclaimed marsh in this estuary.

The greatest need has been to make ecological information available to coastal engineers, and the Department of Environment commissioned ITE to produce a 'Coast dune management guide' expressly for this purpose. It is also important to review coastal management advice, and Anglesey County Council, for example, commissioned a report on the success of management activities over a 10-year period.

D. S. Ranwell

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ECOLOGICAL PERSPECTIVES OF AMENITY GRASS RESEARCH

Any area of grassland which is not used primarily for agricultural purposes can be called an amenity grassland. Such grasslands form a diverse and widespread resource in the UK, covering nearly 4% of our land area. Hence, ITE's research on amenity grassland is broadly based, ranging from the recreation of herb-rich swards (Wells & Bell 1978) to studies of wear on intensively managed sports turf (Gore & Cox 1979). However, these grasslands, whatever their usage, are all ecological systems composed of a variety of species, many of which are not grasses. The balance between desirable and undesirable species in these systems, and hence the quality of the established grass sward, is determined by the outcome of such ecological processes as competition and nutrient cycling, and it is through these processes that management tools such as mowing, fertilizer applications, herbicides and growth regulators operate to control turf structure and performance. If, therefore, we are to optimise management regimes to minimise costs and maximise turf quality, the nature of these ecological processes must first be understood. In the current research programme, ITE is particularly interested in the processes of population dynamics, soil water movement in relation to root growth, and nutrient cycling.

The population studies have been mainly concerned with the dynamics of grass populations during the establishment phase of sports turf. Turf is usually sown with a mixture of species and cultivars, and at seed rates far in excess of the density of plants that would survive under natural conditions. For instance, a seed rate of 25 g m^{-2} would not be regarded as excessive, and yet this figure corresponds to a density of 15 000 seeds $m^{-2}$of *Lolium perenne* and 375 000 seeds m^{-2} of *Agrostis tenuis*. Consequently, the effects of inter- and intra-specific competition on plant growth and mortality are potentially very important in determining the structure of the established turf. The competitive effects have been studied in a field experiment involving just 2 species: ryegrass (*Lolium perenne* cv.S.23) and timothy (*Phleum pratense* cv.S.48). Both species have a good wear tolerance and can be sown on areas such as football pitches where durability is required, but, whereas ryegrass is the most commonly used turfgrass in the UK, timothy is much less popular. The 2 species were sown in all combinations of 7 seed densities (ranging from 0·8 g m^{-2} to 50 g m^{-2}) and 5 species proportions (ranging from 100% ryegrass to 100% timothy), and the growth and survival of grass plants during establishment were then monitored (Parr 1981).

The main effect of intra-specific competition was a reduction in average plant size. Although shoot biomass in the established turf was independent of seed rate, there was little density-dependent mortality at high population densities. It seems that the process of self-thinning, which is so characteristic of plant populations sown at high densities, does not occur in closely mown turf in which there is little or no competition for light. Consequently, the result of sowing a turf at a high seed rate was an established turf with a large number of small plants. Introducing a competitor species further depressed plant size (Figure 42) but had no significant effects on plant mortality. The outcome of inter-specific competition between the ryegrass and timothy was determined by their relative growth rates during the early stages of establishment. In early spring, ryegrass seedlings were 6 times larger than those of timothy, and this early pre-emption of space resulted in an increased proportion of ryegrass in the established turf. Thus, although the standing shoot biomass of a pure timothy turf was 30% greater than that of pure ryegrass, a turf derived from a seed mixture of 50% ryegrass contained 69% ryegrass after the first year of growth.

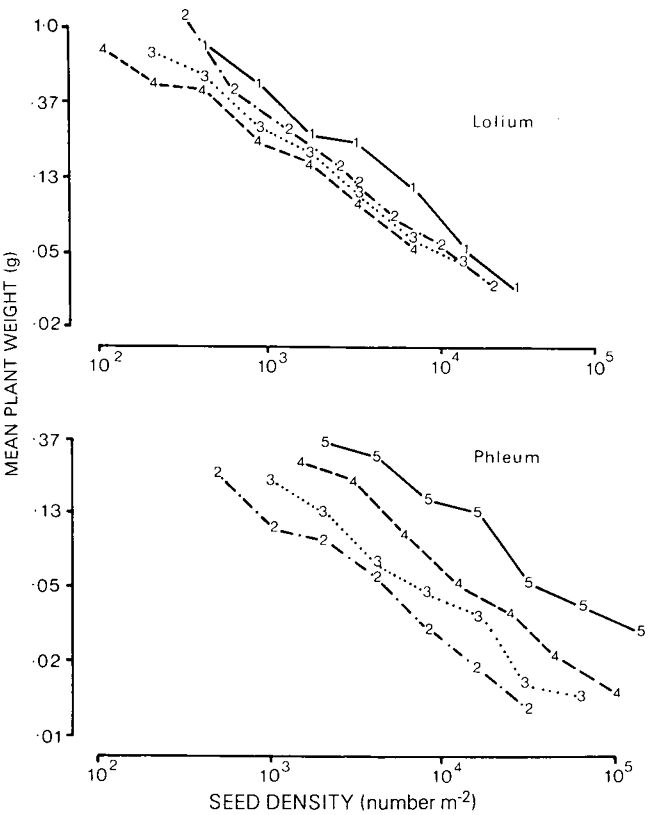

Figure 42 Relationship between initial seed density and average plant weight one year after sowing for (a) Lolium perenne *and (b)* Phleum pratense. *The* Lolium *to* Phleum *ratios in the seed mixture are indicated as follows: 1 = 100:0, 2 = 75:25, 3 = 50:50, 4 = 25:75, 5 = 0:100.*

However, are differences in the population structure of a turf important to turf performance? Although it is well known that some species are more resistant to wear than others (Gore & Cox 1979), there is no information on the effects of plant density and plant size, and a wear treatment was therefore applied to the experimental plots, using a DS2 wear machine developed by the Sports Turf Research Institute. Over the course of a winter, the treatment caused an average reduction in shoot biomass of about 80%, but the loss was significantly greater in those plots from high seed rates; a doubling of seed rate gave a relative decline of 9% in shoot biomass after wear. Evidently then, large plants are more resistant to wear than small plants. Relationships of this kind between seed density, plant size and performance could be important, not only for deciding on appropriate seed rates, but for interpreting trials in which cultivars may establish themselves at different plant densities.

A model of turf establishment is now being constructed to predict the population structure of a turf from the composition of the seed mixture. The model should provide turf managers, at present faced with a confusing choice of many hundreds of grass cultivars, with objective criteria for selecting a particular seed mixture and sowing rate. The general application of the model will be limited because it is based only on the above-ground part of the ecosystem, whereas the dynamics of grass shoots in a short turf are mainly the result of root competition for limited resources, such as water and nutrients. For complete understanding of turf dynamics, we must therefore look below ground, and future studies will examine grass root systems in relation to soil water status and nutrient cycling.

Soil water is an important factor in the performance of amenity turf for 2 main reasons. First, high soil water content resulting from inadequate drainage is the main reason for the poor wear resistance of many of our turf areas. Second, soil water influences the structure of the turf both directly, in terms of growth, and indirectly, through its effect on nutrient cycling. Studies on soil water will use a neutron probe to measure changes in soil water content under different management regimes, which can then be related to root growth and root competition. This information will be used as the basis for a multidisciplinary study on nutrient cycling.

T. W. Parr and Ruth Cox

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Soil Science

GEOCHEMICAL CYCLING IN AN UPLAND GRASSLAND ECOSYSTEM

This project is concerned with transfers of nutrient elements within soil profiles and from soils into fresh water. During 1980, detailed work has centred on a small, first order stream (catchment area 6·5 ha) in the headwaters of the River Wye, near Plynlimon, in mid-Wales. The stream rises at an altitude of 460 m in blanket peat, but the remainder of the catchment is dominated by stagnopodzol soils derived from the mudstones of the underlying Silurian Frongoch series. The peat has a *Molinia-* or *Calluna*-dominated vegetation, while the stagnopodzols are associated with a *Nardus-Festuca* grassland. Total rainfall for the study year 1980 was 2680 mm.

Stream water is sampled weekly and stream flow is recorded continuously using a V-notch weir and drum recorder. Water conductivity is monitored with a probe and recorder (developed by the ITE engineering section) linked to an Epsylon data logger. The instrument is used primarily in conjunction with 'Northants' automatic water samplers to study the chemical response of the stream to specific storm events. Within the catchment, soil water samples are collected for analysis using porous cup soil solution samples (Stevens 1981a), while tray-type lysimeters collect water from the peat and organic surface horizons. Rainfall chemistry is monitored by specially designed collectors (Stevens 1981b), quantitative precipitation data being provided by the Institute of Hydrology.

Results for 1980 show that the stream water is acidic, with a low total ionic concentration (Table 33). The dominant ions are Na and Ca, reflecting the proximity of the site to the coast of Wales.

Two distinct patterns have emerged from the weekly results for the stream water chemistry. NO_3 and K, for example, show minimum concentrations during the

Table 33. Chemical constituents of stream water at Plynlimon for 1980. Mean concentrations are given as mg $litre^{-1}$, except where indicated

Na	3·08
K	0·09
Ca	1·12
Mg	0·72
Fe	0·01
Mn	<0·01
Al	0·02
P	<0·02
NO_3-N	0·08
NH_4-N	<0·50
SO_4	1·71
Cl	4·85
HCO_3 (μeq/1)	54·51
TOC	2·00
pH	5·36
Cond (μS)	34·30

summer months (June to August), with peak levels occurring in winter (Figure 43). Similar patterns are shown by the soil solution data. It seems probable that available NO_3 and K are utilized by plant growth during the summer, whereas, in the winter, these ions are lost from the system in the absence of plant uptake. Si and Ca, however, show a general inverse relationship with stream flow. Peak concentrations occur during periods of low flow, whilst dilution occurs at high water levels (Figure 43). Again, these patterns are also reflected by the soil solution data.

Correlations between flow and concentration are poor, however, probably because of the input of water to the stream from 2 major, but distinctly different, sources, which have been identified as (i) the peat at the head of the catchment, and (ii) the lower soil horizons and weathered bedrock. Water from the latter source was sampled during a period of low base flow in May 1980, when the peat ceased to yield water.

The hypothesis regarding 2 contributing sources has been tested by a simple 2 component mixing model relating concentration to flow (Johnson *et al.* 1969; Cryer 1980). The model has successfully predicted the general behaviour of a number of ions, in particular Na and H^+.

B. Reynolds

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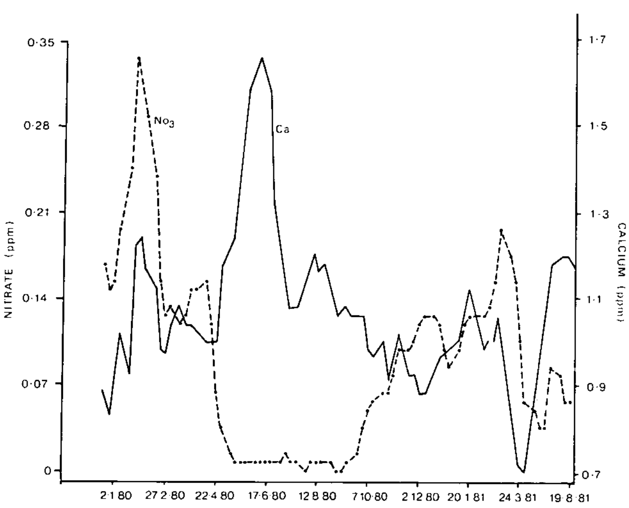

Figure 43 Seasonal changes in nitrate and calcium in stream water from uncultivated pasture on Plynlimon.

PREDICTIONS OF CHANGE IN MOORLAND VEGETATION

(This work was largely supported by Department of Environment funds)

The pattern of heath and rough grassland vegetation on moorland in relation to the distribution of farms, woods and forest is a prominent element in the visual character of the hills and uplands of England and Wales. Changes in this vegetation pattern are a major topic in the debate over the impact of alterations in land use and management on what are often viewed as the 'traditional' and desired landscapes of the hills and uplands.

An investigation of vegetation change between grassland and heath in 12 scattered parishes, forming 4% of the total area of hill and upland in England and Wales, was contracted by the Department of the Environment (DoE) (Ball 1981; Ball *et al.* 1981a, b, 1982). As part of this study, the gains or losses of moorland, and the future changes in the proportions of semi-natural vegetation were predicted for the study areas as a whole, based on assumptions of the effects of agricultural expansion or decline or of forestry expansion. Although detailed classes of vegetation were identified, they are amalgamated here into 4 groups as a summary: improved pastures, rough pastures, grassy heaths and shrubby heaths, with emphasis on the last 3 groups.

Past and present vegetation

Analysis of old maps showed that moorland *c* 1800 in the 12 areas was about 51 000 ha, the remaining 23 000 ha being improved pasture and woodland. Since 1800, moorland has been reduced by about 6%, some of the losses to improvement being offset by reversion of improved pastures. The moorland core, where there is no evidence of previous improvement, has been reduced by about 12%. Recent independent studies have emphasised that the rate of moorland loss has accelerated in many areas over the last 30 years (Parry *et al.* 1981).

From maps and air photographs, the current area of moorland, both moorland core and reverted farmland, was calculated to be 48 000 ha. The vegetation at almost 1000 sites in the study areas was recorded in 1977–78, and the proportions of semi-natural vegetation of the moorland were estimated from these data as 23% rough pastures, 32% grassy heaths and 45% shrubby heaths (Figure 44).

Future moorland vegetation

If agriculture continues to expand at its present rate for the next 20 years or so, the improvement of moorland and associated increases in grazing pressure would reduce the area of moorland in the study areas to about 43 000 ha, a loss of about 10%. Based on the expected response of the vegetation at the sample sites to increased grazing in the individual areas, the characteristic moorland heaths would be particularly affected, shrubby heaths occupying about 40% of the moors, with rough pastures and grassy heaths about 25–35%.

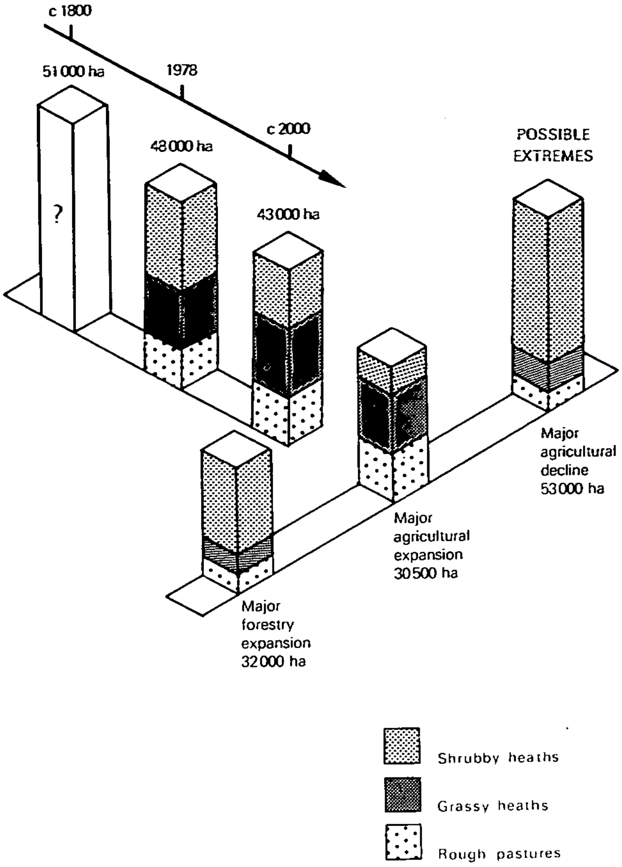

Figure 44 The predicted area and vegetation composition of moorland in 12 upland areas given various trends in land use. The most likely trend is a continuation of the recent pattern of change in the study areas up to the year 2000. The effects of a major expansion of agriculture or forestry, and major decline of agriculture are shown as possible extremes. The major change represents the degree of land use change which has occurred in some areas in the past, but which is envisaged as applying to all areas simultaneously.

Alternatively, agricultural expansion could proceed to the maximum potential of the land, as occurred in some parishes in the past. Such an expansion would leave only 30 500 ha of moorland, a loss of more than 33% of its present extent. The surviving area would retain a similar balance of vegetation to that of the moorland remaining after less drastic agricultural intensification (30–40% rough pastures, 40–50% grassy heaths and 20% shrubby heaths). With continuing and maximum expansion of agriculture, the area of the main groups of moorland vegetation (grassy heaths plus shrubby heaths) would be reduced by 10–50% in the study areas as a whole, but the visually important heather-dominated vegetation could be reduced by 70% of its current present state. The losses would vary regionally, from almost total disappearance in the relatively warm and dry southern and eastern uplands to substantial survival of heath vegetation in the wetter, colder north-central hills.

A third scenario is for a substantial increase in forestry, while retaining agriculture in the most favoured land types. Calculations assuming retention of moorland only on land above 427 m (1400 ft) suggest that 32 000 ha of moorland might remain, a loss of 25% of its 1977–78 extent. As the remaining moorland would be dominated by shrubby heaths, this vegetation group would be almost as common as in 1977–78, but would be largely confined to the higher ground, while rough pastures and grassy heaths would virtually disappear.

Finally, economic pressures could cause a decline in agriculture without forestry expansion. In this case, moorland would probably increase by some 11% to give somewhat more moorland that was present in *c* 1800. The vegetation balance within this expanded moorland is estimated as 10–20% each of rough pastures and grassy heaths and 70% shrubby heaths. Such a scenario would increase shrubby heath frequency by about 50%, but, with the ecological constraints on conversion of pasture to shrubby heaths, the balance would take many decades to achieve.

It is concluded, therefore, that, although the focus of debate is frequently on the loss of moorland, vegetation change within the remaining moorland could result in equally large losses of visually important components, particularly shrubby heaths. The predictions have been made from assumptions that are unlikely to be applied uniformly, but they indicate the limits within which moorland change may occur over the next 20–50 years in the study areas, and, by inference, in the hills and uplands of England and Wales in general.

D. F. Ball

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BOTANICAL EVIDENCE IN THE SOIL OF RECENT VEGETATION HISTORY

Most evidence about soil development and vegetation succession in time is obtained from interpreting existing spatial sequences of soil and vegetation as though they represented changes in time at a single point (the 'chronosequence' approach). Because of the problem of organising repeated measurements in time, as well as the undesirability of waiting for scores, or even hundreds, of years for results, evidence from chronosequences is likely to continue to be the major source of information.

Even when the main interest is in soil rather than vegetation change within a chronosequence, it is still necessary to examine recent vegetation history in order to interpret the soil change. In the absence of, or to supplement, documentary evidence, plant parts and remains in the soil are a valuable source of evidence.

In a current study of the effects on the soil of birch colonizing heather moorland using a series of aged birch stands (Miles & Young 1980), evidence about past vegetation cover has been obtained from stem fragments of *Calluna vulgaris*, viable seed and pollen buried in the soil. No attempt was made to look for phytoliths.

Stems of *Calluna* and viable seeds of this and other moorland species not present in the existing field layer, eg *Erica cinerea*, *E. tetralix* and *Trichophorum cespitosum*, were abundant in the soils of most birch woods investigated. The pattern of declining abundance of stem fragments and seed of *Calluna* with increasing age of the birch stands indicates decay with time of an original *Calluna* cover and non-replenishment of the soil seed 'bank'. As an example, Table 34 gives the numbers of buried stem fragments and viable seeds of *Calluna* at a site near Cannich (National Grid reference NH 325295).

In surface soil under most birch stands, ericaceous pollen predominated over that of birch, usually comprising more than 40% of the total pollen and indicating the former existence of heather moorland (Table 35). Most birch pollen values were less than 10%, indicating the former absence of birch wood. Under mature birch, gradients of an increasing proportion of ericaceous pollen and a decreasing proportion of birch pollen with increasing depth also indicated the recent replacement of heather moorland by birch wood.

Collectively, these botanical indicators give a detailed picture of vegetation changes during the past 50–90 years at the sites studied. Together with information about intrinsic soil homogeneity across sites (eg Hatton 1980), they provide the necessary basis for the assumptions underlying the chronosequence approach to our study on the influence of birch on moorland soils and vegetation.

J. Miles and W. F. Young

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APPLICATION OF THE P-DEFICIENCY BIOASSAY TO TREES

Can the P-deficiency bioassay (Harrison & Helliwell 1979), developed on tree seedlings grown in pots, give useful information on the phosphorus nutrition of forest trees? To answer this question, surface roots of 3 forest stands on peat were sampled during June–July 1980, 2 of lodgepole pine (Clocaenog and Moor House), and one of Sitka spruce (Clocaenog). The stands have received varying levels of phosphorus in fertilizer trials. Detached root samples (less than about 2·5 mm diameter) were assayed to estimate the rates of uptake of ^{32}P-labelled phosphorus, which are assumed to be directly related to the phosphorus deficiency of the trees:

Table 34. Numbers m^{-2} of buried stem fragments and viable seeds of *Calluna vulgaris* in the top 5 cm of soil below L and F layers at a site near Cannich bearing a successional gradient from moorland to mature *Betula pendula*

	Heather	17-year old birch	25-year old birch	69-year old birch	LSD at 5% level
Stem fragments	575	644	394	161	154
Viable seeds	10900	6070	2280	1150	6200

Table 35. Pollen of birch and ericaceous species present at 3 different depths in the soil (expressed as percentage of total pollen) in a successional gradient from moorland to mature *Betula pendula* at a site near Cannich

	Soil depth (cm)	Heather	17-year old birch	25-year old birch	69-year old birch
Birch	0–2·5	4	9	9	15
	2·5–5·0	6	7	9	9
	5·0–7·5	7	5	8	5
Ericaceous species	0–2·5	87	79	72	60
	2·5–5·0	86	80	69	70
	5·0–7·5	82	85	71	72

Fertilizer treatments, tree heights and percentage P contents of first whorl needles have also been compared.

As an example, the data for the lodgepole pine stand at Clocaenog (Table 36) show the uptake rates compared with tree height and P concentration in needles for different fertilizer applications. Both tree height and rate of phosphorus uptake reflect the phosphorus fertilizer applications, despite equal applications of fertilizer in 1979. The needle analyses, on the other hand, show no significant differences between fertilizer treatments, suggesting that the root response in the bioassay may be a more sensitive assay of tree nutritional status than needle analysis.

Surface root samples have also been taken and assayed from Norway spruce, growing either as pure stands or in mixtures with Scots pine, alder or oak, in the Gisburn experiment on a humic gley soil, but with no fertilizer applications. Although there is little, if any, effect of the oak mixture, the rates of ^{32}P-labelled phosphorus uptake by the Norway spruce roots grown in the presence of Scots pine and alder are considerably lower than those for pure Norway spruce, whereas height growth of spruce is appreciably enhanced by these 2 species (Figure 45).

The relationship between spruce height and P uptake is statistically significant (r= -0·72*), and the relationship is improved if the apparently aberrant value for Norway spruce/oak of Block II is omitted (r= -0·90**). The results suggest that the growth of Norway spruce is stimulated in the presence of both pine and alder by changes in its phosphorus nutrition. No needle analyses are yet available for comparison with the ^{32}P-labelled phosphorus uptake by roots.

These preliminary results suggest that the P-deficiency bioassay can indeed be usefully applied to forest stands.

A. F. Harrison, J. Dighton and A. H. F. Brown

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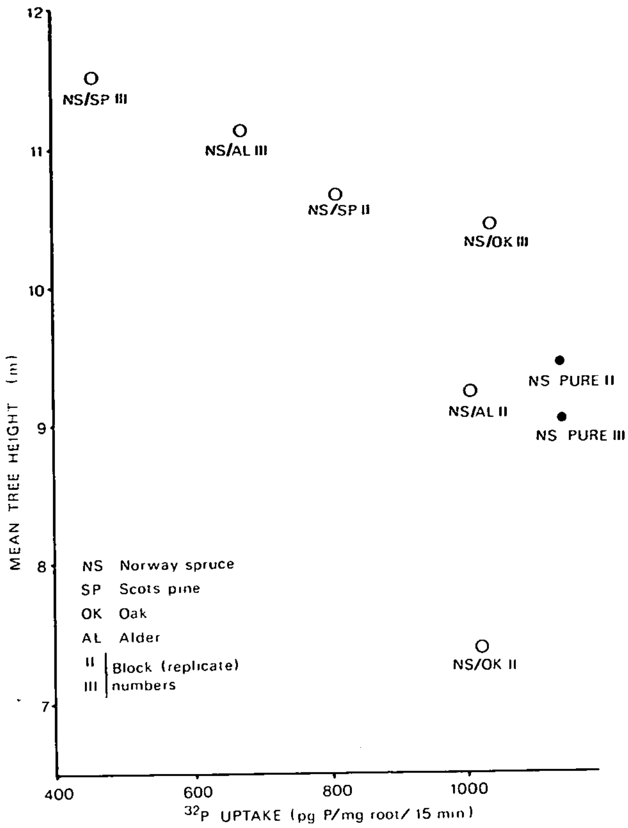


Figure 45 Relationship between tree height and uptake of phosphorus by excised roots of spruce grown pure or in mixture: Gisburn, 1981.

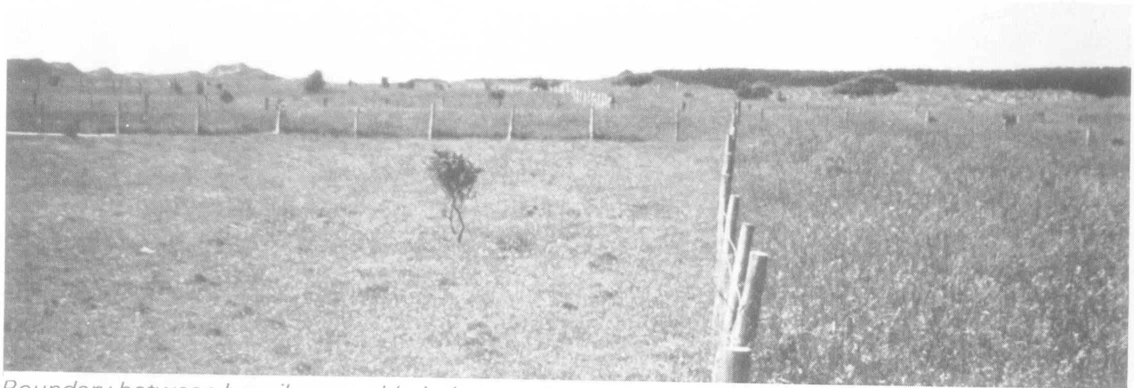
STUMP DECOMPOSITION

At thinning and clear felling of coniferous forests, the normal pattern of litter input to the decomposer cycle is supplemented by a pulse of green needles, live branches, stumps and roots. The additional live substrates have higher nutrient, soluble organic fraction and water content than normally senescent material, and thus a potentially higher rate of decomposition and nutrient release. At thinning, the increased amount and

Table 36. Fertilizer treatment, P uptake rate, tree height and needle analysis of 18-year old lodgepole pine

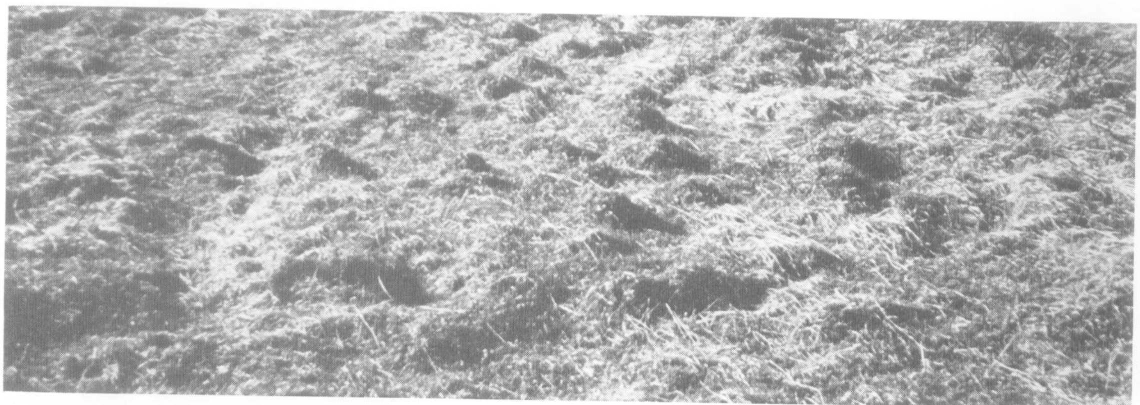
	P fertilizer (kg P ha^{-1})			P uptake (pg P mg^{-1} root 15 min^{-1})	Mean tree height (m)	P in needles (%)$^{+}$
1965	1971	1979	Total			
25	0	50	75	155 ± 11*	5·38 ± 0·13*	0·20
50	0	50	100	124 ± 11	5·86 ± 0·17	0·22
25	25	50	100	124 ± 33	7·18 ± 0·14	0·24
50	50	50	150	61 ± 6	7·69 ± 0·14	0·22

*Standard error; + on bulked samples



a

Boundary between heavily grazed (whole year, 8 sheep) and ungrazed (control) plots. July 1981.



b

Dead Arrhenatherum *tussocks in heavily grazed plot. February 1982.*

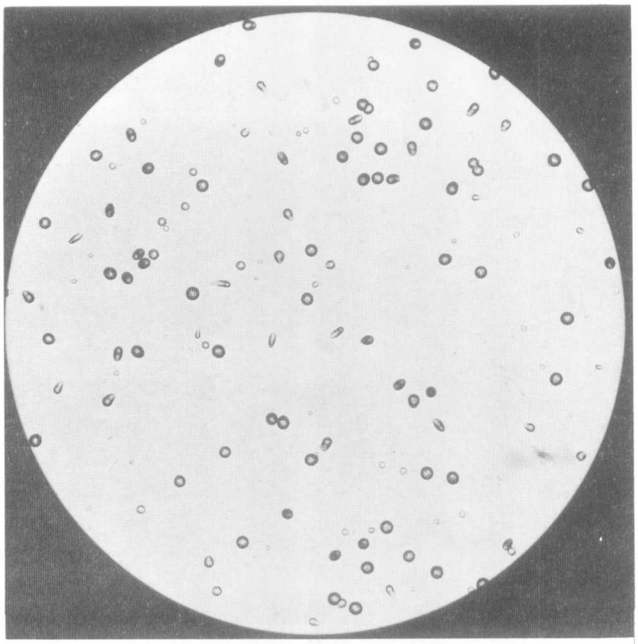
c

Close-up of dead decaying Arrhenatherum *tussocks. February 1982.*

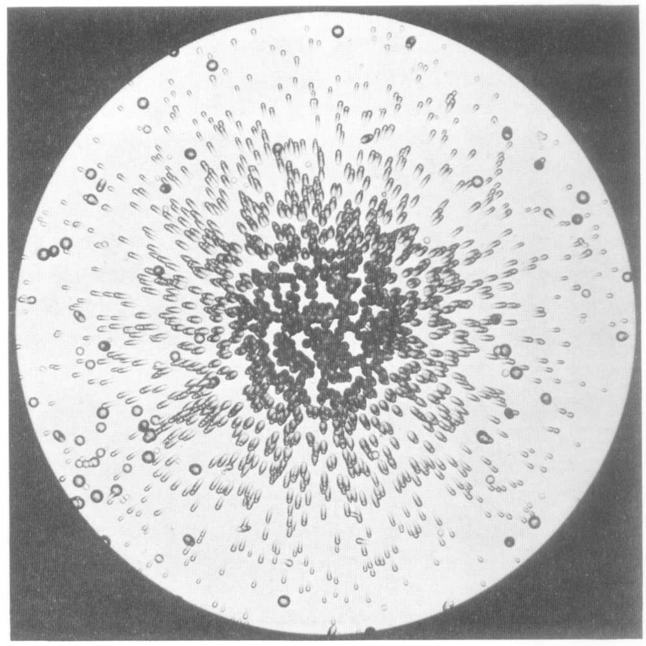
d

Sheep damage to wind-pruned birch tree (Betula *sp*). *February 1982.*

Plate 12 — Newborough Warren grazing experiment.
Photographs D. G. Hewett.



a



b

Plate 13—Photomicrographs of tracks obtained by isotropic recording of the activity of Ravenglass silt using CR-39.
The left-hand photograph shows the kind of field commonly observed, with random tracks typical of the decay of single ions or small groups of atoms scattered through the sample matrix. The right-hand photograph shows a 'hotspot' with its characteristic sunburst pattern of activity. The source in this case is a relatively large particle about 100 microns in diameter.
Photograph C Quarmby.

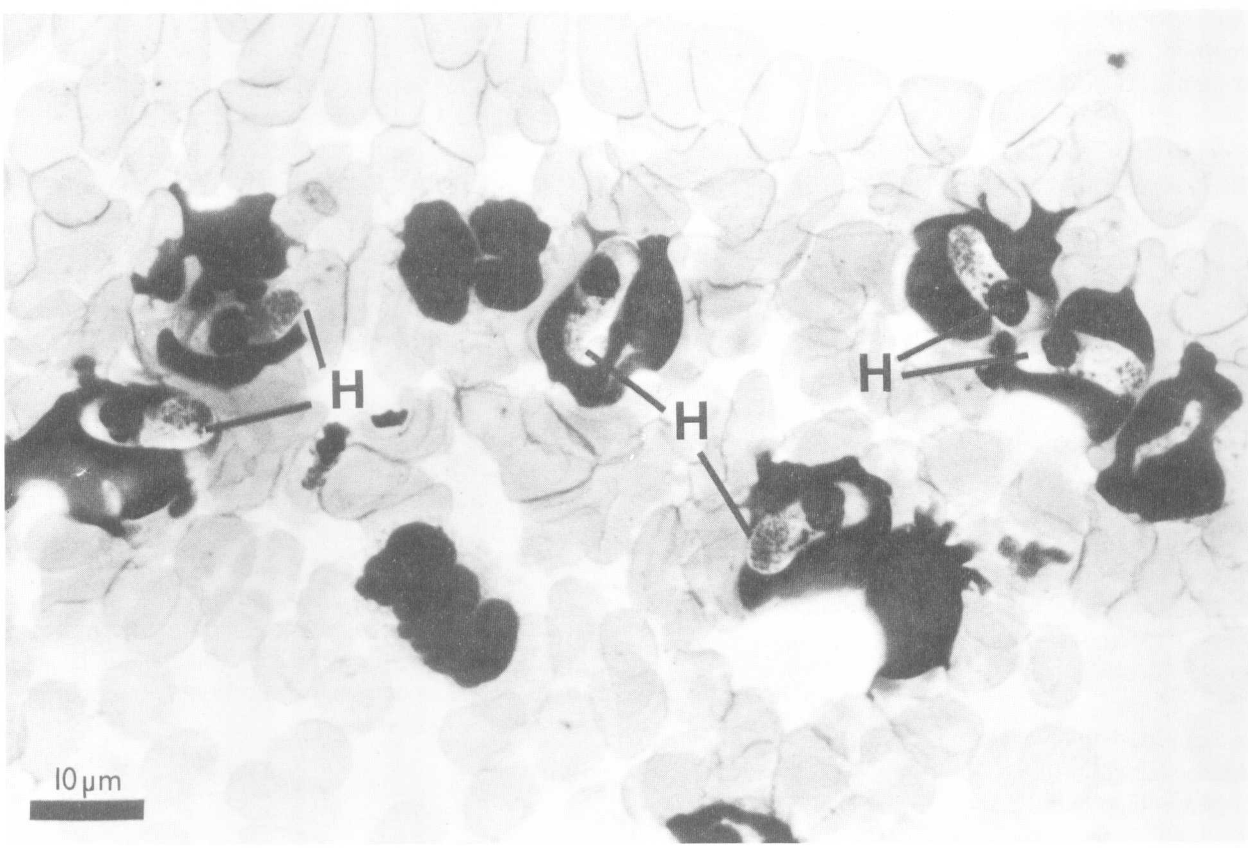


Plate 14—Photomicrograph of 6 Hepatozoon sciuri *(H) in leucocytes of* Sciurus carolinensis *from Monks Wood. Giemsa-stained thin blood film; scale = 10 µm.*
Photograph J. R. Baker.

rate of nutrient release probably contributes to the increased growth rate of the remaining stand, but nutrients released at clear felling are not taken up by plants until the ground vegetation and second rotation are established — hence the frequently-observed increase in nutrients in runoff after felling.

One factor in the dynamics of nutrient release and uptake is the rate of decomposition of tree stumps. The stumps are poor in nutrients compared with other plant parts, and, because of their available carbon and energy, they may act as a nutrient sink in the forest, nutrients being translocated into the stump by decomposer fungi from adjacent sources, eg needles. Thus, stumps may act as a site for the accumulation and slow turnover of nutrients, while needles constitute a site for rapid release. In terms of forest management, such sinks and sources of nutrients may be important for the planting of the second rotation crop, a common practice being to plant against the stump.

As a preliminary to the research project on effects of clear felling (ITE project 625), a small study on the decomposition of stumps of Sitka spruce was used to test methods and obtain initial estimates. To overcome the problem of the long timescale for stump decomposition, sites were selected where thinning had been done at known times in the past, giving an age series of stumps. Sites at Elwy and Dyfi in north Wales and Gisburn and Grizedale in north-west England provided suitable material with up to 20 years since thinning. The density of samples from the stumps, estimated from water displacement and dry weight, was used as a measure of the stage of decomposition.

As expected, there was a high degree of variation in density both within and between stumps; for example, in a fresh stump from Elwy, the density of 6 samples of sapwood ranged from 0·32 to 0·45 g cm^{-3} and 6 samples of heartwood from 0·33 to 0·73 g cm^{-3}. The variability within stumps remained high during decomposition, but the variation between stumps cut at the same time in a site was marked. For example, 2 10-year old stumps in Elwy showed densities of 0·09 ± 0·02 and 0·35 ± 0·05 g cm^{-3}. Such variation within a site may be related to moss cover and moisture retention.

The degree of variability obscured the effects of different sites and any clear trends in the rate of decomposition, but these preliminary data indicate a minimum decay rate, ie decrease in density, of about 1% per year and a maximum of about 5%.

The most interesting result, however, was the change in nutrient concentration. The initial concentration of nitrogen in freshly cut stumps was 0·04 – 0·06%, equivalent to a C:N ration of about 1000. Although there was no marked change in concentration with time since felling, concentrations rose considerably as density decreased (Figure 46). Some of the increase is expected as carbon is lost through microbial respiration and nitrogen is retained in microbial cells. If all the initial nitrogen was retained, the concentration would rise to about 0·18 as the density decreased to 0·1 g cm^{-3}, as shown by the line in Figure 46.

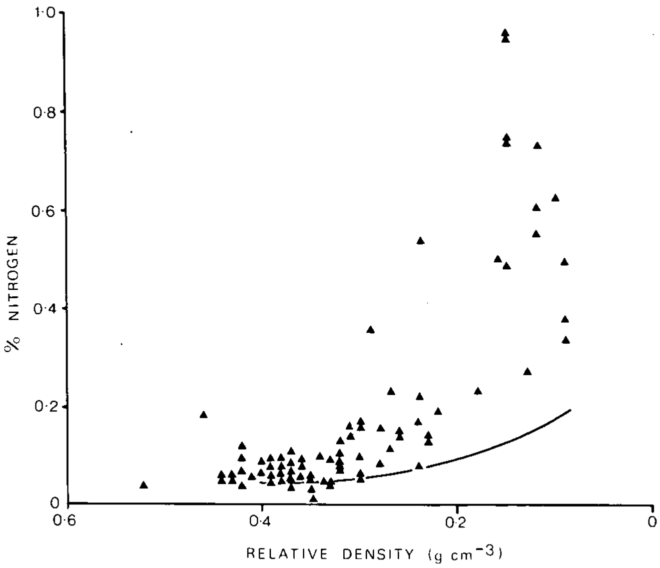


Figure 46 Accumulation of N in decomposing stumps of Picea sitchensis. *The relative density is a measure of the stage of decomposition, freshly cut stumps being 0·4 – 0·5 g cm^{-3}; thus, a relative density of 0·1 represents a mass loss of 75 – 80%, reached 10 – 20 years after felling. The line represents the change in concentration resulting from decomposition if there was no addition or loss of the initial N content (from Heal* et al. *in press).*

However, concentrations were 2 – 5 times higher than expected, ie there was an increase in the absolute amount of nitrogen as the stump decomposed. Such increases in absolute amounts are regularly observed in decomposing organic matter, but rarely to the degree found in the Sitka spruce stumps. Although nitrogen fixation may be occurring, the parallel increase in phosphorus indicates retention of nutrients in rain or translocation by fauna and microflora from adjacent litter which is relatively nutrient-rich.

Despite the difficulties in determining the rate of decomposition, the preliminary results indicate that stumps act as sinks in which nutrients are accumulated for at least 10 – 20 years.

Kathryn Newell and O. W. Heal

Reference

Heal, O. W., Swift, M. J. & Anderson, J. M. In press. Nitrogen cycling in United Kingdom forests: the relevance of basic ecological research. *Phil. Trans. R. Soc. B.*

Data and Information

SERVICES

Computing

The integration of the Institute computing into the NERC Computer Services (NCS) is complete and functioning. However, there is still a need for the Institute to maintain a policy overview. In practice, NCS resources have been such that there has been a necessity to assist NCS staff with local software development, and the Subdivision of Data and Information has therefore maintained a major interest in computing. Among the services provided have been data base management advice and programming, routine statistical programming and specific mathematical modelling software. More specialist work by members of the Subdivision has involved the development of software for digitising map data using cheap and robust digitising equipment, and software for relating remotely-sensed digital data (ie Landsat data) to land use patterns in Snowdonia and northern Kenya.

Biometrics

The Subdivision continues to support the research of the Institute by providing biometrical advice, on both experimental design and data analysis. Although seriously under-staffed, the policy of providing biometrical advice in each station was implemented as far as possible, involving the redeployment and movement of staff to locations where needed.

Remote sensing

The increasing use of remotely-sensed data in land use and vegetation studies has been considerably helped by collaboration with the Experimental Cartography Unit (ECU) of NCS. ECU has recently acquired an I^2S image analysis system, which ITE has been using to explore the relevance of remote sensing to land use problems in Britain and overseas.

The vegetation of the Snowdonia National Park has been surveyed extensively by staff at the Bangor Research Station, and these ground-captured data are being compared with Landsat imagery and their relevance evaluated. In addition, Landsat imagery is being compared with other land classification methods, particularly that of Buse (1974) and Bunce and Shaw (1980).

Although the use of Landsat imagery is well-developed for extensive survey in developing countries, ITE is currently using these techniques for detecting incipient desertification in northern Kenya. This methodology has been developed from similar work on the increase of erosion in the Snowdonia National Park.

C. Milner

References

Bunce, R. G. H. & Shaw, M. W. 1980. National woodland classification. *Annu. Rep. Inst. terr. Ecol. 1979*, 106.

Buse, A. 1974. Habitats as recording units in ecological survey: a field trial in Caernarvonshire, north Wales. *J. appl. Ecol.*, **11**, 517–528.

Biological Records Centre

1. Botanical recording

During the past year, the botanical activities of the Biological Records Centre have been completely reviewed. As a result, a programme has been devised to restructure the botanical records to make them broadly compatible with the reorganised zoological schemes. Some parts of the programme have already been implemented; others will be adopted gradually during the coming years.

The data pathways for vascular plant records have been revised in close collaboration with the Botanical Society of the British Isles (BSBI), who have appointed a scheme organiser. The recorders have been advised of the changes, and the scheme organiser and BRC coordinator have attended relevant BSBI meetings. The plant records will be reconstructed in parallel with this programme, and the accumulated backlog of records incorporated. Distribution maps are being produced for the forthcoming 5-volume Flora of Great Britain and Ireland.

Two genera, *Carex* and *Hieracium*, have received special attention during the past 2 years. Maps for the second, enlarged edition of the BSBI *Carex* Handbook have been produced, following the revision of our records on some critical taxa by appropriate specialists. More recently, we have begun to computerise the *Hieracium* records, again in collaboration with specialists, and the computer file has been designed to suit the special requirements of botanists interested in this group. *Hieracium* is the most difficult genus in the British flora, and all the records are based on critically determined specimens.

The fifth volume of the Atlas Florae Europaeae was published in 1980, with British records contributed by BRC. Records for the next 2 volumes, which will cover the Caryophyllaceae, have been submitted. In 1981, the first part of the Atlas of Lichens of the British Isles was edited and prepared for publication, and maps of Myco-mycetes, to be published as a provisional atlas, were also produced. Preliminary plans have been made for the Bryophyte Atlas, to be produced when the current phase of the British Bryological Society recording scheme comes to an end in 1982.

A special computer file for records of Charophytes has been created in collaboration with the British Museum (Natural History), and provides details of locality, determiner and habitat. A provisional card for diatom recording has been designed. The taxonomy of this group is so uncertain that the normal species-orientated approach is not possible: the computer file will give an index of collections with accompanying information on water conditions. Diatoms are useful indicators of habitat conditions, and can thus be used to trace the environmental history of a lake. A register of collections will provide an index of available data.

2. Zoological recording

During the last 2 years, the reorganisation of the Centre, described in the ITE Annual Report for 1979 (p. 119), has been consolidated, and contact has been strengthened between the organisers of recording schemes and the BRC co-ordinators.

Three general recording cards ('One Species', 'Individual Record' and 'Other Species'), which are available for use by all schemes, have been redesigned and printed in A5 size. All recording cards produced after 1979 have been designed to obtain a standard minimum set of information with each record, and have also been printed in A5 size by the NERC/SRC Reprographic Services. New cards are available for Tricladida; Odonata; 4 groups of Coleoptera — Coccinellidae, Cerambycidae, Bruchidae and Chrysomelidae; Elm Scolytidae; Trichoptera; Lepidoptera Oecophoridae; Aculeate Hymenoptera; and Tardigrada. A draft recording sheet was designed for a new scheme covering Diptera Culicidae, and will be used in a one-year trial before a recording card is prepared. Five of the above cards are for new schemes, and 3 of them, together with the sheet of Culicidae, contain some system for recording details of habitat or biology.

Data now held on computer file include records of marine Dinoflagellata; freshwater Hirudinea; non-marine Mollusca; Diplopoda; Orthoptera; Lepidoptera — Rhopalocera and macro-Heterocera; Diptera — Dixidae; Hymenoptera — Apidae; non-marine Isopoda; and Opiliones. Data on Chilopoda, Odonata, Pseudoscorpiones, Mammalia, Reptilia and Amphibia are being edited prior to input. Data on about 300 species of Lepidoptera — Noctuidae have been edited, and maps are being produced at the Rutherford Computing Laboratory.

The Atlas of Bumblebees was published in 1980, together with revised provisional Atlases of Odonata, Orthoptera, Hymenoptera — Vespidae and Hymenoptera — Formicidae. In 1981, a provisional Atlas of Marine Dinoflagellates was published, using the new marine base map produced by BRC late in 1979. This marine base map uses the Universal Transverse Mercator (UTM) grid, and covers the western Atlantic from longitude 24° West to 12° East and latitude 48° North to 65° North. The Atlas of the Butterflies of the British Isles (to be published jointly by ITE and NCC) is in preparation, and the maps for it have been fully edited. Maps for various species of vertebrates were updated, and 17 maps prepared for a provisional Atlas of Hirudinea to be published by the Freshwater Biological Association. Various preliminary distribution maps were sent to recorders, including those for 227 species of Lepidoptera, 4 species of *Asellus* (Isopoda) and 28 species of aquatic Coleoptera.

Acting on behalf of the European Invertebrate Survey (EIS), the first part of the Provisional Atlas of the Invertebrates of Europe was prepared and published in 1981. The Atlas contains maps of 27 species of Lepidoptera, Hymenoptera and Nematoda. On his retirement, the secretariat of the EIS will pass from J. Heath to Mr M. Meyer of the Natural History Museum in Luxembourg.

J. Heath, P. T. Harding, Dorothy M. Greene, C. D. Preston and H. R. Arnold

RESEARCH

The birds of Shetland — a computer-based checklist

During the Shetland survey (Milner 1975), considerable quantities of literature were searched for background information. It was felt that this information should be held in a more structured form, and a computer information system seemed appropriate. In view of their importance in Shetland, birds were chosen as the first group for this approach, and a checklist has been published (Hamilton 1981).

The checklist currently has 3 main sections:

1. an alphabetical main list of species and subspecies with at least one reference per entry;
2. a list of book references organized geographically;
3. a list structured ecologically.

In order to produce the alphabetical main list, 15 previously published checklists have been collated and cross-checked to produce a composite list with documentary evidence to support inclusion of a species or subspecies in the new list. In addition to the 3 main lists, there are lists in systematic order (Voous) and also an indication of the status of the species on Shetland (either breeding, non-breeding, or rare).

The lists have been compiled and stored as disc files on the PDP-11 computer at Merlewood, using BASIC programs, which has greatly facilitated the production, expansion and upgrading of records as new material became available. This facility can obviously be used in future as additions or changes are needed.

Although the checklists are useful in themselves, it is hoped that the information stored can be used for biogeographical research. Examples of the sorts of classification possible are shown in Tables 37 and 38.

Table 37. Examples of possible classifications

	No of species
1. Breeding species: resident + migrant past + present	115
2. Non-breeding species: regular migrants	67
3. Non-breeding species: nationally rare	156
4. Non-breeding species: locally rare	63

Table 38. Analysis of the breeding birds of Shetland according to abundancy class, and in relation to the British breeding numbers (1977)

Class No	(British Isles) Breeding pairs		BI	Sh	%
1	1	9	10	2	20
2	10	99	21	8	38
3	100	999	22	9	41
4	1000	9999	46	23	50
5	10000	99999	34	32	95
6	100000	999999	29	22	76
7	1000000+		13	10	77
8	Sporadic breeders		14	4	29
9	Others		–	5	–

Similar work on other groups is planned.

C. Milner

References

Hamilton, N. 1981. A bibliographically-annotated checklist of the birds of Shetland. (Merlewood research and development paper no. 84). Grange-over-Sands: Institute of Terrestrial Ecology.

Milner, C. 1975. The Shetland project. *Annu. Rep. Inst. terr. Ecol. 1974*, 64–66.

Severn tidal power pre-feasibility study

(This work was largely supported by Department of Energy funds)

One of the main purposes of the pre-feasibility study was to narrow the choice of schemes by eliminating those clearly shown to be less economic than others (Department of Energy 1981). Many contractors, covering a wide range of activities, were involved, but NERC was mainly concerned with tides and their modelling, and with the environmental impacts of building a barrage, ie effects on the quality of tidal waters, on flood protection and land drainage, and on ecological systems and nature conservation. The Subdivision considered how systems analysis in general, and modelling techniques in particular, had been used, or could be used, to study the environmental impacts.

A wide range of environmental studies had been carried out on the Severn estuary during the pre-feasibility stage, but ecological modelling activities had been limited to the simulation models of the Institute for Marine Environmental Research (IMER) for use in water quality and ecological studies, and a carbon flow model of the estuary's salt marshes and mud-flats, developed by the University of Wales Institute of Science and Technology (UWIST). The pre-feasibility study had not been identified with the use of systems analysis as an overall approach, and, as a consequence, it was not possible to produce satisfactory whole-ecosystem models once the data had been collected and the study designed.

The main conclusions were that multidisciplinary teams should be set up at the outset of any future studies, that ecosystem concepts should be exchanged at an early stage, and that there was unlikely to be a single, comprehensive model suitable for the whole estuary. It was suggested that a systems analysis study of the Severn tidal power proposal was most likely to result in a series of linked modules, and that the key factor in the success of any future studies was likely to be the development of mechanisms whereby the individual modules could be linked together.

D. K. Lindley and C. Milner

Reference

Department of Energy. 1981. *Tidal power from the Severn estuary.* (Energy paper no. 46). London: HMSO.

Chemistry and Instrumentation

INTRODUCTION

This report of the Subdivision of Chemistry and Instrumentation is divided, as in previous years, into 2 parts, one dealing with the service activities and the other with research and development studies. In comparison with most of the projects described in this Annual Report, the work of the service staff at first appears tedious and of limited interest. It is certainly not easy to produce an exciting and interesting report about routine production work. However, many of the day-to-day problems encountered by the service section are surprisingly complex and require a considerable amount of skill in their solution. Furthermore, in many cases, they have to be dealt with rapidly because of production pressures or to meet a promised delivery time.

Examples of the type of problem dealt with by service staff are referred to in the service section reports. In the Merlewood analytical contribution, mention is made of the need to clarify solutions prior to analysis of starch and carbohydrates. This brief statement masks an exhaustive investigation during which the effectiveness of adsorption, precipitation, flocculation and centrifugal treatments had to be checked, in conjunction with interference and recovery tests. Similarly, at Monks Wood, the task of analysing small samples of aquatic organisms for low concentrations of heavy metals involved a considerable amount of patient and meticulous work.

The position with the other support groups is similar, in that they also have to deal with complex, intractable and unexpected problems. The engineers, perhaps more than the other staff, are constantly on call to get an instrument working, to make a device at short notice, or to modify some equipment to meet changed specifications. In the case of the nursery staff, a considerable degree of responsibility is also involved, because they have to maintain heated glasshouses and ensure that plants are kept in good condition for experimental purposes. Even photography, the smallest service, is occasionally called upon to tackle unusual requests, or to meet a deadline.

The Subdivision of Chemistry and Instrumentation, perhaps more than any of the other Subdivisions, depends a great deal on access to specialised equipment, much of which is in heavy use and, in some cases, fully automated. The difficult financial situation has meant that replacements have been less easy to obtain, which has meant that time has had to be spent on keeping some instruments operational beyond their normal life expectancy. So far, the only major loss has been the complete breakdown of the flameless atomiser instrument at Merlewood. Fortunately, it has been possible to transfer some of the work depending on this instrument to the Monks Wood laboratory, where similar facilities are available. In contrast, the radiochemical service, as a relatively new group, has not had to deal with problems of instrument deterioration. In this case, most of the difficulties have arisen because of the need to get instruments commissioned and techniques in operation, in order to meet the requirements of the radionuclide research team.

The second section of this Subdivision report ranges from exploratory research, as in the study of pine needle surface properties (pp. 93–95), through to the potential of a new technique for examining alpha emitters, and development work carried out to improve mist propagation practice. In the case of engineering, some of the large construction jobs completed during the year are of sufficient magnitude and complexity to justify full description under individual reports. The contrasting nature of the research reports from this Subdivision is a reflection of the many disciplines it covers.

Not all the research projects covered by the Subdivision are dealt with this year, as some were described in recent Annual Reports, eg the project on aquatic pollution (ITE 481). No reference is made to the studies on chemistry of waxes (ITE 710), which are being carried out in connection with the sulphur pollution programme, although one of the research reports (pp. 93–95) does deal with the way that pollution damage can be related to the 'wettability' of pine needle surfaces.

This year, it has been possible to present the first progress reports of the recently-established radionuclide group. This team is looking at certain aspects of the distribution of radionuclides in the terrestrial environment, largely under contract from the Department of the Environment (DoE). The first of these contract studies, dealing with the distribution of radionuclides in a salt marsh in west Cumbria, was completed towards the end of 1981, and a summary of the findings is given below.

S. E. Allen

SERVICES

Analytical chemistry, Merlewood

The major techniques for nutrition and pollution analysis of ecological materials are well established, and are the essential bases for processing the large numbers of samples produced by the ecologists of ITE. However, new research projects require that techniques are reviewed, and new methods are developed accordingly.

No increase in throughput of samples was achieved this year, mainly because of the labour-intensive nature of some of the requirements. Many small batches of soil samples for a full range of tests proved to be extremely time-consuming, as were the determinations of proximate constituents required by several projects. However, a considerable reduction in the backlog of work was achieved by careful control of commitments, which had the added benefit of allowing more flexibility for urgent project work, and new research developments.

Two investigations, concerned with geochemical cycling at Plynlimon (ITE 594) and clear felling of a site at Kershope forest (ITE 625), have generated water samples for regular monitoring. Samples requiring anions such as phosphate or nitrate are analysed immediately, because of the labile nature of the constituents, and, as these 2 projects alone produced about 3000 samples over a 6-month period, some congestion at the instrumentation stage was inevitable.

Two major contracts handled during the year were associated with research work being carried out in the Antarctic region. About 400 soil samples were examined by Dr M. B. Usher of the University of York, as part of the study into the distribution of soil arthropods in the Antarctic.

Analyses of vegetation (1500) and soils (100) were also carried out for biologists of the British Antarctic Survey under a regular analytical support agreement. Some rather unusual analytical problems were encountered in this work, because of the physical reaction of the sample material. Some of the lichens were very brittle and springy, causing difficulties during the sample preparation stage, and very finely divided lignin fractions were obtained from some of the grasses, quite unlike anything met before. In addition, the wide range of material types and nutrient element concentrations resulted in dilution and digestion problems.

The method most generally used for assessing nitrogen availability in soils measures the amounts of total nitrogen released after incubating the soils for about 14 days. Although this method has been widely applied, it has some limitations, especially for soils with a low nitrogen content. It does not take into account the rates of release and continual utilisation of the nitrogen. Investigations into the significance of these processes in tundra soils have been carried out by Dr K. Van Cleve (ITE 712), a visiting scientist from Alaska, and the analytical section has been involved both in the development work and in the processing of the test samples. These investigations are continuing.

Although most of the samples coming into the laboratory needed processing for nutrient elements, many different types of organic analyses were also carried out. Particular problems that had to be dealt with included the development of proximate techniques for a range of faecal materials, methods of stabilising and clarifying pine needle extracts prior to starch and carbohydrate analyses, and the fractionation of organic nitrogen in grouse food and droppings. This latter study (ITE 130), carried out in association with Dr R. Moss of the ITE Banchory Research Station, called for the separation of free ammonia, amino and amide nitrogen, uric acid, urea and ornithuric acid.

A recurrent problem during the year resulted from equipment breakdown, and a considerable amount of time has had to be spent in keeping equipment in operation. Most serious of all has been the total loss of the furnace atomiser used with atomic absorption. All urgent low-level work has had to be transferred to the Monks Wood laboratory, which has put more pressure on their already-overloaded system.

J. D. Roberts, H. M. Grimshaw and A. P. Rowland

Analytical chemistry, Monks Wood

This year the laboratory has continued to be concerned mainly with the analysis of avian materials and aquatic organisms, with the emphasis on heavy metal determinations. The principal metals of interest have been cadmium, lead and zinc, although occasional tests were carried out for other metals. Because of the small size of many of the samples, especially the aquatic materials, it has generally been necessary to use an atomic absorption spectrophotometer, equipped with a graphite furnace atomiser and automatic sample presentation. Through the use of this technique, it has been possible to correct for sample contamination.

The laboratory has been involved in investigations into swan poisoning since 1973, when lead was found to be the cause of a swan mortality on the River Trent. During the current year, swan tissue samples have been sent from East Anglia, and levels of lead in the livers ranged from 90 to 200 mg kg^{-1} dry weight. The lead mainly orginates from fishing weights and shotgun pellets.

The demand for organochlorine analyses has continued, the emphasis this year being on dieldrin (HEOD), DDE and polychlorinated biphenyls (PCBs) in eggs and tissues of seabirds and birds of prey as part of the ITE/NCC monitoring study.

The anodic stripping analytical technique, mentioned in the 1980 Annual Report, has been in regular use throughout the year for the determination of di- and trialkyl lead compounds in avian tissues (ITE 181). The performance of the equipment has been improved, however, by the construction of a new cell and electrode assembly by the station engineer. This new apparatus incorporates a vibrating 'stirrer-plate' positioned beneath the glassy carbon (working) electrode. The vibrating plate is driven by a solenoid activated by a variable pulse electronic control circuit. The improved efficiency of solution mixing, over the conventional magnetic spin-bar stirrer, has more than tripled the sensitivity of the method.

M. C. French and K. R. Bull

Radiochemistry

The radiochemical laboratory facilities were completed in late 1980, and much of 1981 has been spent developing the techniques which are now in use for the analysis of soil, silt, vegetation and animal materials for both α- and γ-emitters.

The counting facilities consist of 2 high-resolution lithium drifted germanium (Ge(Li)) semi-conductor detectors for γ-spectrometry and 8 silicon surface barrier detectors for α-spectrometry. All these detectors generate data which are handled simultaneously by a multichannel analyzer. In addition, a sodium iodide crystal scintillation detector is available for lower resolution γ-spectrometry, although this detector can only be used at the expense of an α-detector.

Three standard geometries are in routine use for the analysis of γ-emitters using Ge(Li) detectors. These are:

i. 150 ml polystyrene tub.
ii. 50 mm diameter petri-dish.
iii. 1 litre capacity, well-type Marinelli beaker.

Methods (i) and (ii) can be used for either high- or low-active material, depending on the amount of sample available, although low-activity samples in a petri-dish require long counting times, and this combination is only used in exceptional circumstances. Method (iii) is used for low-activity samples, where a large amount of material is available. Standards of suitable activity are prepared once or twice a year, by spiking examples of each sample type with a mixture of γ-emitters designed to cover the range of energies of interest (50 – 200 KeV). Efficiency tables are generated for each sample type and these are checked every 2 or 3 months. To facilitate throughput and to avoid changing samples at unsocial hours, counting times have been standardised at 25 000 secs ($\sim$7 hours), 60 000 secs ($\sim$16 hours), 80 000 secs ($\sim$24 hours) and 175 000 secs ($\sim$48 hours). The time chosen depends on the activity of the sample and the need to satisfy counting statistics. Spectra are quantified by recording on to floppy discs and processing in batches on the station PDP-11 computer. Analyses for α-emitters require a complex chemical separation to isolate the element of interest prior to α-spectrometry. Procedures have been adopted for determining isotopes of plutonium and americium. The methods are subject to constant development, as more experience is gained of the various stages involved, and also of the different characteristics of the sample types examined. The original procedure chosen for plutonium was found to be satisfactory for the higher levels in west Cumbrian salt marsh silt and vegetation, but had limitations when samples with lower activity were analysed. Modifications had to be made to the electrodeposition stage, and also to one of the precipitation stages, which have improved recovery efficiencies so that the method can be applied routinely in most cases.

^{241}Am, although an α-emitter, is determined by γ-spectrometry, using the 59·5 KeV line if at all possible. However, levels below about 5 pCi g^{-1} have to be determined by chemical separation and α-spectrometry, as the γ-activity is too low for acceptable quantitative estimations. A procedure based on anion-exchange in the thiocyanate form is being adopted, which should give clean separations and recovery efficiencies of around 50%.

J. A. Parkinson

Engineering

This year, the trend in engineering has been towards smaller construction tasks and repairs to existing equipment, the latter need being dictated by severe financial constraints experienced in 1981. It has, however, been possible to embark on a few major construction tasks which will be mentioned later in this report.

The structure of the section is unchanged from last year, with a central unit of 3 engineers at Bangor, and an engineer at all other stations except Furzebrook and CCAP. The Bush and Monks Wood engineers were able to provide workshop training for a number of young people under the work experience programmes, and in turn benefited from the extra assistance. An industrial trainee student from Huddersfield Polytechnic spent 6 months in the Bangor workshop.

The engineer at Bangor assigned to station tasks has provided considerable support for the soil science team working on contract for the National Coal Board (NCB) (ITE 727). There has also been a constant demand at Bangor for a wide variety of field testing and sampling devices. One major task has been the fitting out of a sample preparation room for communal use, which has involved the provision of all services, including compressed air and dust extraction facilities. Maintenance work on station has also been demanding, due especially to equipment repair.

Engineering support requests at Monks Wood were mainly mechanical and electromechanical, and ranged from the design and construction of kestrel traps to the automation of water distillation equipment for the chemical laboratory and Animal Function Subdivision. Some modification to the anodic stripping apparatus for estimating low levels of heavy metals was also carried out.

At Merlewood, the largest proportion of the engineer's time was spent on servicing and repairing equipment and on building maintenance. Modifications to the glasshouse included special staging and the provision of automatic trickle watering and air circulation (ITE 553). The engineer was able to devote some time to the development of a system of controlled environment chambers for a study of leaf photosynthesis (ITE 674).

Bush and Craighall Road are both served by the engineer at Bush. The largest construction tasks this year have been the design and fabrication of filter units for use with the open-top chamber (ITE 380, Bush), and the construction of traps for lampreys (ITE 676, Craighall Road). Building maintenance at both stations and the supervision of people employed by the Manpower Services Commission for workshop practice have also been features of the duties carried out in the year.

Further development work on radio telemetry and tracking transmitters was carried out by the engineers at Brathens (ITE 687), and, together with repairs to tracking receivers and aerial systems, occupied a large part of the time during the year. The remaining time was spent on minor electrical and mechanical support duties.

G. H. Owen

Plant culture

1. Glasshouse developments

As an energy conservation measure, the heating system in the high-energy consumption glasshouses at Bush has been changed from electric fan heaters to gas-fired low-pressure hot water. Because of the large volume of water in the heating pipes, response to changes in temperature is a little slower than with electric air heating. Consequently, the thermostats controlling the various heating and ventilation systems had to be readjusted relative to each other to avoid a 'heat-on/ventilators open' condition, and a wider temperature range for each of these glasshouses has now to be accepted. Another recent development has been the installation of 3 stand-by diesel generators to provide an emergency power supply for essential equipment, eg heating controls and mist benches.

During 1981, the nursery unit carried out work in support of 14 projects, 4 of which are from other ITE stations, apart from Bush. The plant population is now 37 000, and the increase in research under glass forced the unit to seek relief accommodation in glasshouses of 2 other research institutes on the Bush estate.

In order to improve the production figures for clonal multiplication of tree species, all vegetative propagation work carried out by project staff was transferred to the nursery section where the necessary expertise was available. Placing this specialised work under one experienced member of staff undoubtedly contributed to the 50% improvement in production.

2. Field plots
In order to reduce maintenance costs, particularly on labour and herbicides, more of the plantings at Roslin and Glencorse Mains (field plot sites, each about 2 miles from Bush) are being laid down to grass using low maintenance ryegrass cultivars such as 'Manhattan', 'Pelo', and 'Sprinter'. This choice is of greatest benefit at Glencorse, where the stony nature of the soil could cause rapid wear of cultivating machinery. In cases where the grass would compete with young plants, 'Treespats' have been used, which are bio-degradable bitumen squares (0·5 × 0·5 m) laid on the ground around the base of the plants to prevent unwanted vegetation. This practice markedly improves the establishment and growth of newly-planted trees in grassland.

Trees planted at Glencorse Mains are generally growing well, and the area appears to be less susceptible to late spring frosts than Bush or Roslin. This site has thus been chosen for a *Thuja mini* seed orchard, as this is a species which can be severely affected by early frosts. A task which was new for the nursery unit in 1981, but one which will involve its staff increasingly in the future, is the removal of redundant trial material. It involves grubbing out semi-mature trees and, where these are growing in grass, has to be done carefully to minimise disturbance of the sward. A small winch is used in this operation.

The amenity grass trial at Roslin for the Sports Turf Research Institute was completed during the year, and the area is now available for a second term of research planting.

3. Landscape design
Local landscape design commissions in the past year have included the screening of modular buildings for the East of Scotland College of Agriculture at a nearby farmstead, the restoration of woodland on a rural tip site for the Edinburgh Centre of Rural Economy, and a survey and review of planting in the policies of Bush House for the Edinburgh Centre of Rural Economy.

R. F. Ottley

Photography
The demand for assistance by the photographic unit has remained steady throughout the year, and has further demonstrated the need for this specialist service. There were, as always, many requests for both black-and-white and colour slides, arising from the frequent lecturing engagements of ITE staff. High quality black-and-white enlargements for published reports were needed on several occasions, and other illustrative work included the provision of colour photographs for ITE publications. In one case, rather more direct research support was provided through the use of photographs to count the numbers of birds of a particular species in specific study areas.

A major undertaking in 1981 was the provision of display material for the Monks Wood Experimental Station open days, which involved the production of 1200 black-and-white captions and diagrams, 70 monochrome prints and 250 colour prints. It was particularly difficult to maintain high quality in the colour work because almost all the prints had to be produced from 35 mm slides. Similar material, on a smaller scale, was provided for the ITE exhibit at the East of England show.

Two internal information reports were issued during the year, one containing recommendations on the production of art work for lecture slides and display material, and another dealing with a new chromogenic dye emulsion film.

P. G. Ainsworth

RESEARCH AND DEVELOPMENT

Monitoring changes in pine needle surfaces

1. Background
The effects of environment on the production by plants of epicuticular wax have been of widespread interest, and have been studied for several different plant species. Such factors as light intensity, temperature, photo-period, water stress, air pollution and herbicides have been shown to be important in controlling the amount of wax, its chemical composition or structural form (eg see Hull *et al.* 1975). There has, however, been little detailed study of the changes in epicuticular wax once leaf expansion is complete and the wax can be regarded as 'mature'. Although the environment may control the formation of the wax and its ultimate com-

position and structure, the subsequent modification of the wax is more likely to be influenced by the direct action of external factors than by the plant itself. These external factors may include physical abrasion by wind-blown dust or by other leaves, temperature, the deposition of particulates, and the chemical effects of pollutant gases and acid rain.

Changes in epicuticular wax may be studied in several ways, the most important to date being electron microscopy. The physical structure and appearance of the wax can be seen to alter with time, after exposure to air pollutants, or after abrasion. On conifers such as *Picea pungens* and *Pinus sylvestris*, the small rodlets of wax appear to become fused, and eventually no fine structure is visible (Reicosky & Hanover 1976; Fowler *et al.* 1980; Huttunen & Laine pers. comm.). These observations are at best only semi-quantitative, but other methods may give a better-defined measure of change.

Schuck (1972) and Schütt and Schuck (1973) monitored the chemical composition of the epicuticular wax of *Pinus sylvestris* throughout a growing season, and observed marked fluctuations in the hydrocarbon, ester and alcohol components. The overall trends showed relative increases in longer-chain hydrocarbons and decreases in esters in 2-year old needles, as compared with one-year old needles, but, as their measurements were relative rather than absolute, it is not clear whether the observed changes were the result of increases in some components or decreases in others. This approach, however, is necessary for any conclusive study of the chemical changes which may occur, in that it should suggest the nature of chemical reactions involved.

A third method measures the contact angle of a water droplet on the leaf surface. The way in which a droplet of water behaves when placed on a leaf surface depends on the 'roughness' of the leaf surface and the chemical composition of the epicuticular wax. On a perfectly smooth surface, the contact angle is governed by the hydrophobic or hydrophilic characteristics of the surface, being large (>90°) or small (<90°) respectively. In general, a distinction must be made between the angle formed at a droplet advancing over the surface and at one receding from a previously covered surface. In practice, it is the 'advancing' angle that is usually measured. The observed behaviour results from the balancing of the surface tension of the drop and the interaction between the water and the surface. The surface roughness has an additional effect in that, if small pockets of air are trapped between the droplet and the surface, the area of contact is reduced and the apparent contact angle may be greatly increased. The 'roughness' may be submicroscopic involving the fine structure of the epicuticular wax (1 – 10 μm), or it may be of the same order as the size of the droplet (0·1 – 1 mm). Changes in either of these 'roughnesses' may be expected to affect the contact angle.

The contact angles of the leaves of many plant species have been investigated, both before and after removing the epicuticular wax by solvent (Holloway 1969). Partial removal of wax by abrasion has also been shown to decrease the contact angle (Hall & Jones 1961). The effect of environment on contact angles has not been studied so intensively, but there is incidental evidence of a reduction in contact angle with time from work by Leyton and Juniper (1963), on *Pinus sylvestris*, and Fogg (1947) has noted diurnal changes and the relationship to water potential. Recent work at ITE Bush has shown not only a marked reduction in contact angle with time, but a significant additional effect of air pollution on the epicuticular wax of *Pinus sylvestris*.

2. Current research (ITE 710)

Pine needles (*P. sylvestris*) have been collected at approximately 10-week intervals, and contact angles measured on 5 needles of 5 trees from each of 3 year classes (current, one-year old, 2-year old). The results from 2 sites are presented in Figure 47. Contact angles were determined by placing a one μl drop of distilled water on the centre of the abaxial surface of the needle which was viewed using a microscope with a protractor

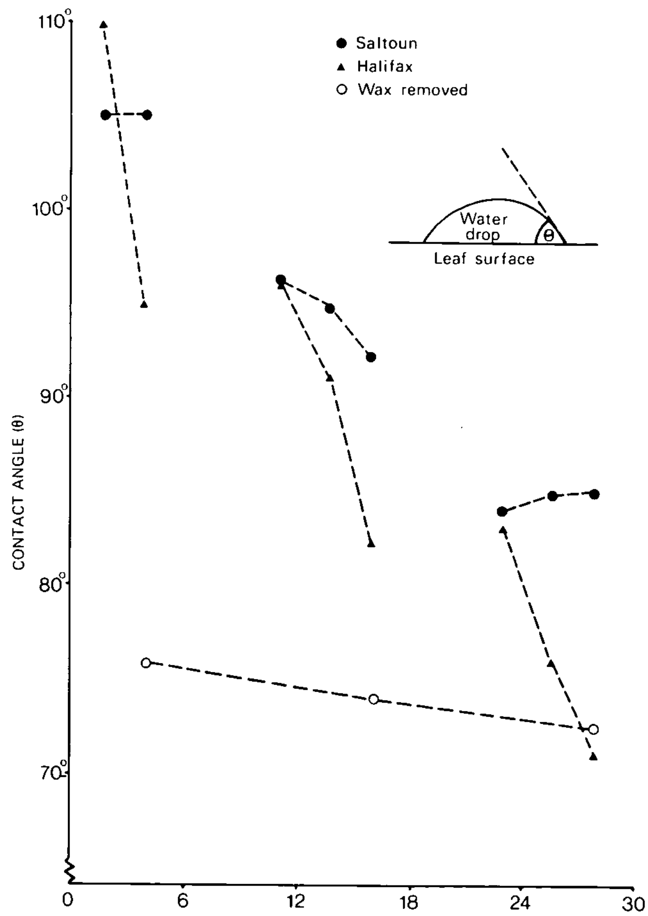


Figure 47 Variation of contact angle with needle age at 2 sites (polluted and unpolluted) and after removal of epicuticular wax.

graticule. The value recorded was an average for both sides of the drop. Also included in the Figure are the contact angles for chloroform-washed needles, showing the contribution of the epicuticular wax to the overall contact angle. Values for washed needles from the 2 sites were not significantly different, and it is interesting that the slight decrease with age may be related to water content of fresh needles, which also decreased with age, from 58% of fresh weight for current year needles to 54% for 2-year old needles (Fogg 1947).

The site at Saltoun (East Lothian) is in a region with little air pollution, at an elevation of 180 m, while the Halifax site is subject to significant air pollution ($\gtrsim$50 μg SO_2 m^{-3}) and is at an elevation of 300 m. All trees sampled were from the same provenance (Altyre).

A third site, also with trees from the Altyre provenance, is situated in the Cairngorms, at an elevation of 380 m, and was used to assess the adverse effects of elevation and exposure. Samples consistently showed greater contact angles than either the Saltoun or Halifax samples, which suggests either that the initial chemical composition of the epicuticular wax was different, or that the increased effect noted in the Halifax samples was the result of air pollution. This question cannot be solved conclusively without the results from a chemical analysis of the waxes, which is in progress, but it was observed that there were large amounts (up to 50 μg cm^{-2}) of chloroform-insoluble 'sooty' material on the surface of the needles from Halifax, which were present to a much lesser extent on the needles from Saltoun. These deposits increased with time.

The observed decreases in contact angle could, therefore, be related either to a change in the fine structure and/or chemical composition of the epicuticular wax, as seen to occur using scanning electron microscopy (Fowler *et al.* 1980), or to a hydrophilic deposit on the needle surface. Undoubtedly, a significant proportion of the observed change is natural and may be ascribed to weathering. Whatever the mechanism of the change in contact angle, the effects are important because the critical value of 90°, below which a needle surface becomes wettable, is reached significantly sooner at the Halifax site. This result has implications not only for water storage by the canopy, but for gas exchange, and further study of the physical structure of the surface, of cuticular transpiration, and of chemical composition is currently in progress.

J. N. Cape

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Analytical technique development

1. Ammonia method

The empirical technique for determining ammonium-nitrogen in ecological materials is by distillation, and many laboratories determine NH_4^+-N in Kjeldahl digests by this method. A colorimetric method, based on the Berthelot reaction, is a generally accepted alternative which is extremely sensitive and specific. However, it is necessary to use automated colorimetry to control the condition of this reaction for precise results.

The Berthelot reaction is complex, and the choice and composition of reagents are numerous. In general terms, ammonium salts react with a chlorine donating agent to form the intermediate monochloramine, which combines with a phenolic compound at high pH to form the indophenol blue dye. Until recently, sodium phenate was used as the phenolic compound, with manganese as the catalyst, but equipment improvements and changes in service requirements have necessitated modifications. For example, recent investigations into nitrogen mineralization, and the large numbers of water samples with extremely low ammonia levels demonstrated that the baseline on the Auto-Analyzer phenate method was too noisy to provide the sensitivity required.

After reviewing recent literature, it was decided to develop a method for NH_4^+-N using sodium salicylate with sodium nitroprusside as catalyst, because they were considered most likely to give the sensitivity required for determining NH_4^+-N in ecological materials. The sensitivity improvement obtained, together with modification to an Auto Analyzer to give a more stable baseline, has achieved a working detection limit of 5 μg $litre^{-1}$.

No interferences were detected, and comparison tests with both plant and soil digests and extracts produced no significant differences between the trial and distillation methods. 0·02 M calcium chloride extracts were found to be troublesome when a phosphate buffer was used in the reaction, but manganese salts which catalysed the phenate reaction did not interfere with the salicylate method at the 1% level.

The pH control of this reaction is critical, affecting both the rate of reaction and the λ max of the indophenol blue. Choice of buffers at pH 12–13 is limited to either potassium chloride or disodium hydrogen phosphate, both of which are potential contaminants in the laboratory. However, likely pH variations in solution handling were found to have no effect, eliminating the need for a buffer.

2. Computing developments

All the software for processing the data from the routine analytical instruments and balances to give weight-corrected results was completed during the year. A facility for compiling the final customer report was introduced, which gave the option of paper tape output on request. Stand-alone BASIC holds a chemical data bank of information on almost 250 different plant species occurring in Great Britain.

A. P. Rowland

Alpha-particles by solid state nuclear track detection

The passage of a heavily-ionising nuclear particle through dielectric material leaves a trail of radiation damage which can subsequently be etched to give a characteristic track. Such tracks can easily be counted and measured under the optical microscope. The simplicity of the technique, together with its low operating cost, has led to its application in numerous fields of science and technology. Particles examined range from protons to the heavy, relativistic ions of cosmic rays, and applications include dating the formation of the solar system, radiation dosimetry, and measuring the height at which birds fly. The work described here has been concerned with recording α-particles emitted from environmental samples, chiefly soil and vegetation, using the polycarbonate plastic CR-39 as the detector material.

The passage of a charged particle leaves a latent track, a cylinder of damage about 10 nm in diameter and up to 1 mm in length, depending on the energy of the particle. After etching, the cylinder becomes a cone, the dimensions of which depend on such parameters as the energy of the particle, its mode of deceleration, the detector material, its uniformity, the strength of the etchant, and duration of etching, but careful control of conditions enables reproducible results to be obtained. After etching, the cone is not longer than the latent track, but is typically 10 μm in diameter at the mouth, an increase of 1000-fold.

The mechanism of cone formation depends on the fact that radiation-damaged material along the latent track is etched away more quickly than the undamaged material, which forms the bulk of the detector. The speed at which the former takes place is referred to as the track-etch rate (V_T) and the latter as the bulk-etch rate (V_B); both are usually measured in $\mu m\ h^{-1}$. Figure 48 shows the manner in which cones of different shape may be produced. The damaged core is etched out quickly, allowing the etchant into the body of the detector, after which the material is etched at the bulk-etch rate. The final envelope after etching can be determined using Huygen's Principle; thus, in (A), if the etching time is t, V_Bt will be etched from the undamaged surface, whilst the total length of the etched track will be V_Tt. The shape of the track is also obtained using Huygen's Principle; thus, if the etchant reaches point P after (1/3)t, then the etchant can act from this centre for (2/3)t. The envelope of this etching sphere, therefore, has a radius of V_B (2/3)t, and so on for all other points along the track. In (A), the latent track is longer than V_T and $V_T/V_B \sim 5$: hence, the etched track is cone-shaped. In (B), on the other hand, the latent track is fully etched out in time t, and moreover, $V_T >> V_B$, so that the time spent in etching out the core is negligible compared to t. These conditions give rise to a cylindrical track of uniform diameter $2V_Bt$. In practice, V_T does not remain constant, but increases as the ionising particle decelerates within certain limits. The effect on the shape and size of the etched cone is compared in (C) and (D). It should be noted that, in this case, the ionising particles have passed completely through the film, so that, on etching, cone formation takes place at both surfaces simultaneously. This effect is commonly observed with the heavier ions.

So far, routine determinations have been confined to measuring the total number of α-particles emitted from a given sample. Samples are ground, pressed in aluminium planchets, and held in contact with CR-39 using a simple clamping system, until a sufficient number of tracks have been accumulated. These tracks are etched and counted using an image analyzer; typical fields are illustrated in Plate 13. Mention has been made of the simplicity and inexpensiveness of the technique. A further advantage is that many samples can be counted at the same time, and they can be held for as long as necessary to obtain a valid count. The method is particularly suited to the investigation of environmental samples where activity is very low. In such cases, counting with conventional equipment ties up expensive instruments for long periods and results in a low throughput. Future work is planned to allow discrimination of the energies of the α-particles by measuring track dimensions.

C. Quarmby

Radionuclides in a salt marsh

A study of the variation of radionuclides in a salt marsh bordering the Esk estuary in Cumbria has been carried out (ITE 553), involving the measurement of radionuclide levels in both the vegetation and the surface layers

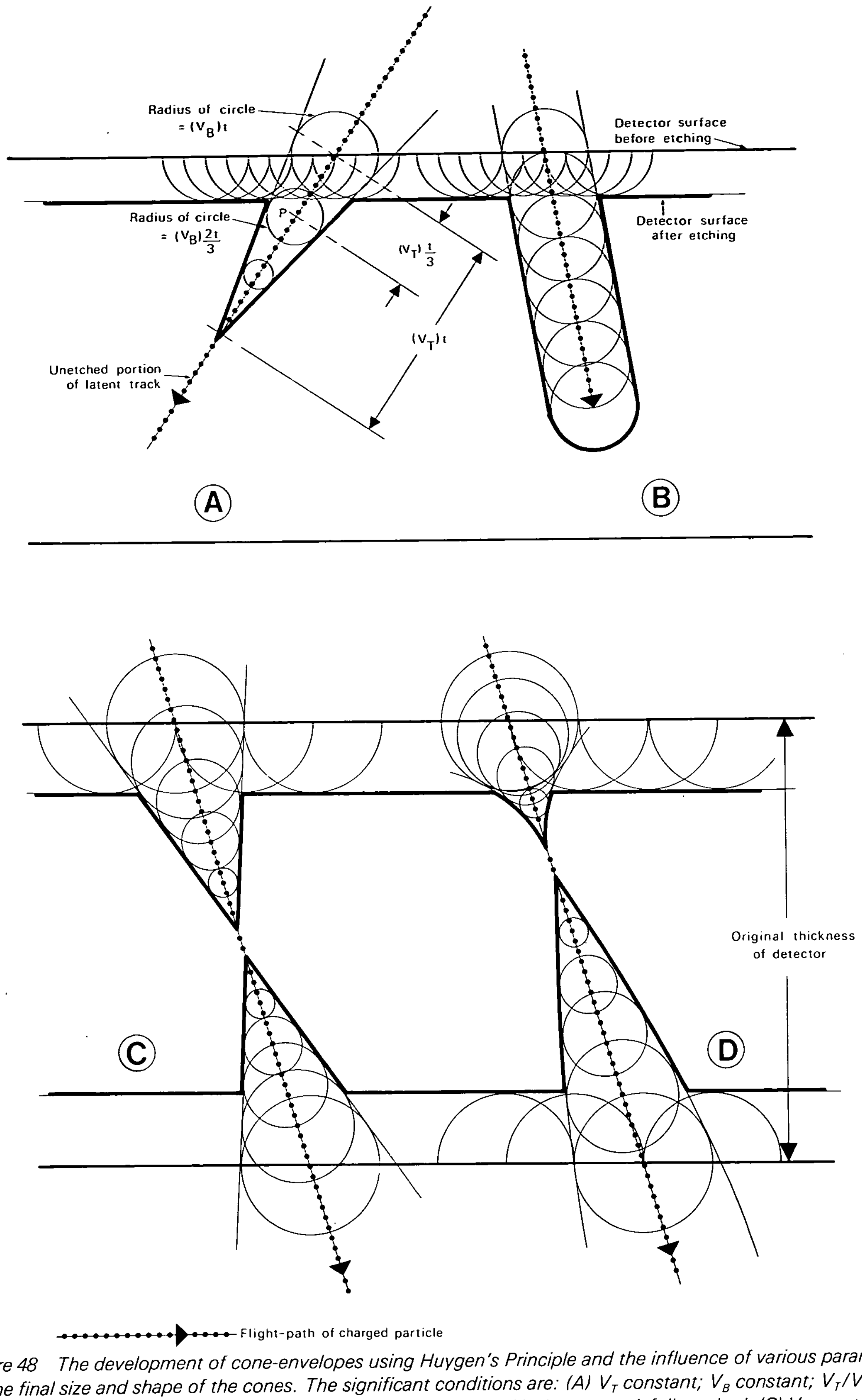

Figure 48 *The development of cone-envelopes using Huygen's Principle and the influence of various parameters on the final size and shape of the cones. The significant conditions are: (A)* V_T *constant;* V_B *constant;* $V_T/V_B = 5$. *Latent track not fully etched. (B)* V_T *constant;* V_B *constant;* $V_T >> V_B$. *Latent track fully etched. (C)* V_T *constant;* V_B *constant;* $V_T/V_B = 3$. *(D)* V_T *increasing;* $V_{T(O)} = 4$, $dV_T/dt = 2$; $V_B = 5$ *and constant.*

of silt. Gamma spectroscopy was used to quantify some of the elements, including ^{241}Am, ^{137}Cs, ^{134}Cs, ^{144}Ce, ^{106}Ru, ^{154}Eu, ^{95}Zr and ^{95}Nb. Wet chemistry, followed by alpha spectroscopy, was used for ^{238}Pu and $^{239+240}$Pu.

As in all salt marshes, the duration of tidal immersion is the main factor in determining the distribution of sea-borne materials throughout the marsh. To examine this distribution, indicator species analysis was used and showed a number of well-defined communities, all correlated with tidal immersion times. These communities exhibit a range of morphological structures, ranging from a short, grassy turf a few centimetres high, mainly of *Puccinellia maritima*, to a bushy vegetation over 0·5 m in size, dominated by *Halimione portulacoides*. There are indications that the structure is important in trapping incoming radionuclides attached to silt particles, as some of the highest levels recorded have been found in the tangled *Halimione* stands.

Concentration of all the elements show positive correlations with height above ordnance datum (OD), ie tidal immersion, with the exception of those with short half-lives, ^{95}Zr (64 days) and ^{95}Nb (35 days), which are negatively correlated with height above OD ($P<0{\cdot}01$). The rate of deposition of these short half-life elements appears to be too slow for a net accumulation to take place.

Overall, the point-to-point variation on an experimental survey grid (Figure 49), where the points were 25 m apart, was large, an important consideration when only a few sample points are used in monitoring studies. For instance, in the surface silts, ^{241}Am ranged from 35–81 pCi g^{-1} in non-vegetated channels and mud-flats to over 250 pCi g^{-1} under stands of *Halimione portulacoides*. Corresponding figures for ^{137}Cs were 50–200 pCi g^{-1} for open areas to over 500 pCi g^{-1} in vegetated stands.

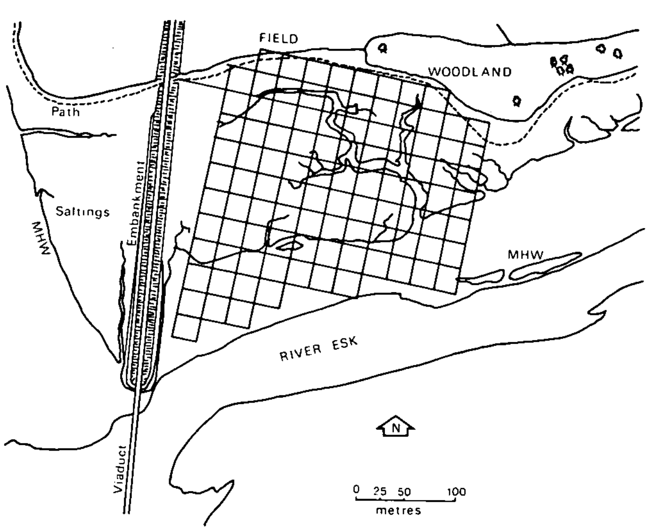

Figure 49 Layout of experimental area at Ravenglass for the study of radionuclide distribution in an ungrazed salt marsh.

Trend surface analysis has been used to investigate overall patterns of distribution on the marsh. Two of the plots, ^{241}Am (half-life 432·2 years) and ^{95}Nb (35 days) (Figures 50, 51), illustrate the trends obtained. For ^{241}Am, a quadratic function ($F=8{\cdot}14$, $P<0{\cdot}01$) is significant and demonstrates the way deposition takes place in concentric zones out from the railway embankment. In contrast, ^{95}Nb shows an essentially linear pattern ($F=34{\cdot}12$, $P<0{\cdot}001$), although the quadratic component ($F=6{\cdot}94$, $P<0{\cdot}01$) adds a little information to the plot.

Similar techniques are being used to look at radionuclide distribution within a grazed salt marsh in the same area, and this study is linked with work being carried out on the uptake of radionuclides by grazing animals.

A. D. Horrill

Radionuclides in sheep

Studies on grazing animals in the vicinity of the Windscale reprocessing plant have concentrated mainly on cattle. For example, milk is routinely monitored as a sensitive biological indicator of variations in stack emissions. Recently, interest was extended to the many sheep grazing the fells to the east of the plant. Some sheep also graze the lowland pastures near the coast.

The grazed salt marsh vegetation around the Ravenglass estuary presents potential sites for the study of radionuclide uptake by sheep. ITE has developed a particular interest in a flock of Swaledale sheep which graze the salt marshes bordering the River Irt in the Ravenglass estuary. Close liaison has been established with the National Radiological Protection Board in this work.

Sheep from the marshes are being analysed at different times of the year, and the feasibility of sampling and analysing sheep food and droppings during the same period is being investigated (ITE 553). As radionuclide uptake is often enhanced in suckling animals, lambs will also be analysed from April to November when they are sold at market. Prior to routine analysis, one 6-year old ewe which had died in advanced pregnancy was obtained to assess the possible difficulties of analysis and the amounts of radionuclides likely to be found in the samples. This sheep has been examined in considerable detail to see whether there is any evidence of radionuclide accumulation and to determine which tissues are sufficiently representative for routine analysis. Hence, individual muscle blocks and different bones are being analysed, as well as tissues such as the diaphragm, adipose tissue and brain.

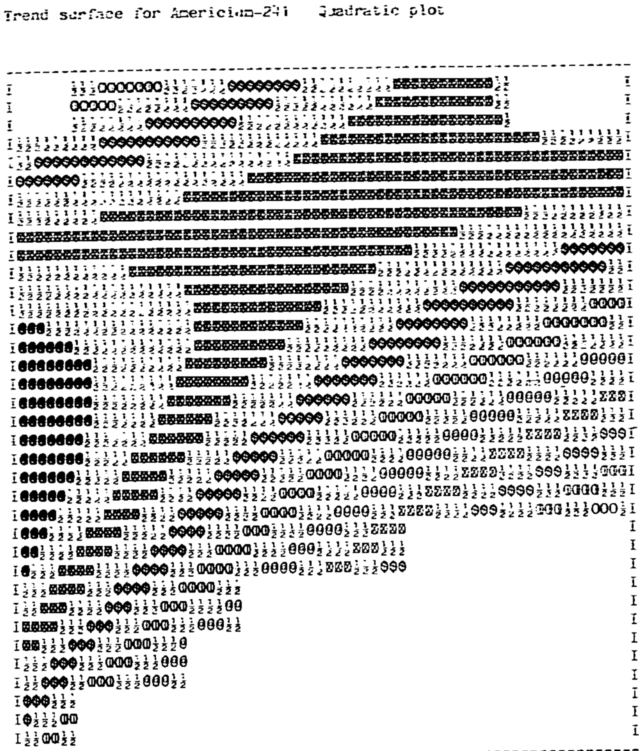

Figure 50 Trend surface diagram for ^{241}americium (half-life 432·2 years) using data derived from the quadratic trend surface equation. Density of symbols is related to concentration of radionuclide in 20 even steps.

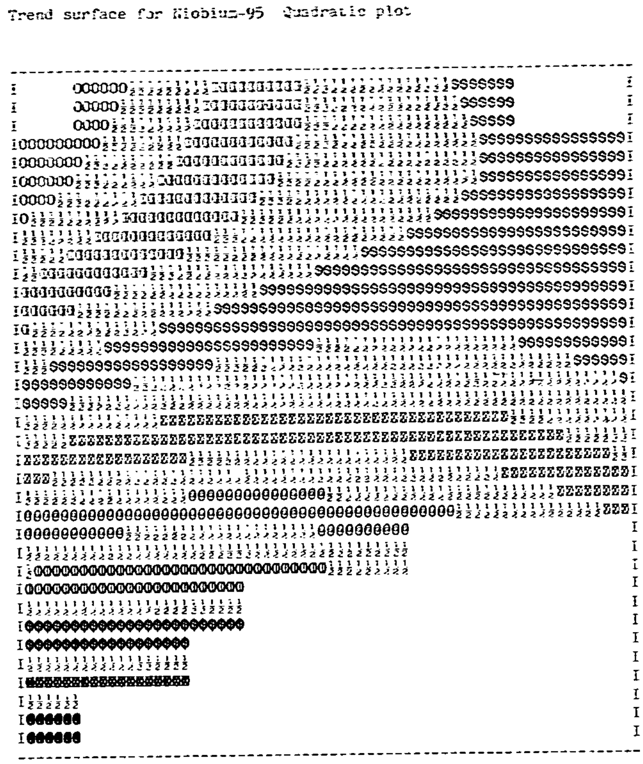

Figure 51 Trend surface diagram for ^{95}niobium (half-life 35·1 days) using data derived from the quadratic trend surface equation. Density of symbol is related to concentration of radionuclide in 20 even steps.

Soft tissues were weighed, minced and freeze-dried at -30°C to -40°C for 2–3 days. Bones were boiled clean, ground to a powder and oven-dried. All samples were then reweighed and ashed in a muffle, at 500°C for 2 – 3 days to concentrate the radionuclides. Radionuclides in the ash were counted using standard geometries on the Ge(Li) gamma detectors for at least 60 000 seconds. Standards containing a range of gamma-emitting radionuclides were prepared to enable quantification of the radionuclides.

One of the main problems of analysing individual tissues was caused by the low levels of radionuclides present, which necessitated long counting times, often more than 175 000 seconds. Even so, examination of the spectra often indicated the presence of other nuclides which were present in insufficient amounts for quantitative analysis without excessively long counting times.

Initial results indicate that, although tissues such as the liver, lungs and kidney take up radionuclides such as ^{137}Cs, ^{106}Ru and ^{134}Cs, as might be expected, other tissues not normally considered may also be of interest. Adipose tissue, for example, seems to accumulate ^{95}Nb, which may be due to the use of fat reserves in winter concentrating the nuclide, or accumulation over a long period coupled with the slow metabolic turnover of fat cells.

Ultimately, it might be possible to relate these studies to the extensive hill areas of less contaminated pastures grazed by sheep in Cumbria.

Brenda J. Howard and K. L. Bocock

Algal growth chambers

Experimental work on the predation of freshwater phytoplankton by zooplankton (ITE 694) requires the use of culture vessels for rearing these organisms. A prototype vessel in clear polycarbonate was produced, which had the advantage of being non-toxic, steam-sterilizable and easy to fabricate. The vessel consisted of a cylindrical moulded tank, flanged at the top end to accept the lid which could be sealed in position. The lid served as a mounting platform for the pair of counter-rotating, speed-controlled, mixing paddles, in addition to the liquid inlet and outlet, heating element, cooling coil and transducer sensors.

The culture vessel operated on the turbidostat principle. A relatively constant turbidity of water cloudiness was maintained by diluting the culture with nutrient solution, when the phytoplankton population reached a preset level. At the same time, a sample of culture was removed to a zooplankton culture vessel. Turbidity was monitored by an infra-red source and detector mounted diametrically across a large bore tube with a rubber piston. A timing circuit actuated the piston at intervals to remove any algal growth from the cylinder walls, and also to ensure that a fresh sample of culture was introduced between light source and detector. The method of turbidity sensing worked equally well under fluorescent lighting or in darkness, providing the culture was sufficiently dense.

Temperature was controlled in the vessel by a water-cooled coil and silica-sheathed heater. A temperature sensor gave an accurate read-out, as well as providing feedback for the temperature control.

G. H. Owen

Environmental chambers for leaf photosynthesis studies

Gas exchange and micro-meteorological observations of vegetation growth were required as part of an energy study into fast-growing biomass (ITE 674). *In situ* photosynthesis measurements of field crops, eg Japanese knotweed (*Reynoutria japonica*) and bracken (*Pteridium aquilinum*), required some compact portable leaf chambers in order to isolate growing leaves for gas exchange analysis. Temperature control, humidity control and air mixing were required within the chambers. Parameters to be monitored included light intensity received by the upper leaf surface, average air temperature within the chambers, and the temperature at the surfaces of the leaf, together with the ambient air temperature of the rest of the plant.

Two perspex leaf chambers have been built to meet the above requirements. Their internal air temperature can be controlled within 0·5°C over the range ± 15°C from ambient. The chamber temperature can also track ambient. Cooling is achieved by semi-conductor Peltier diodes that are clamped to an aluminium heat sink forming the base of each chamber. The diodes are powered from a car battery or portable generator, together with the other control circuitry. Heat extracted from the chambers is efficiently removed from the hot side of the diodes by finned heat pipes. Reversed current flow through the Peltier diodes is used to heat the chambers. This novel approach is more compact and convenient for field use than conventional freon refrigeration with compressor and piping, or cooling by water circulation.

Air inlets and outlets of the chambers are connected to an infra-red gas analyzer via a gas handling unit. All measured variables are conditioned to give direct panel meter readings and continuous recording on a multi-point chart recorder. Interfacing this information to a microprocessor for data storage and analysis is now in hand.

D. G. Benham

Microprocessor studies

During the year, a number of requests were received from project leaders for the design and construction of dedicated microprocessor-based data logging equipment. These requests included an automatic location recorder for animals tagged with radio transmitters (ITE 687) and a field recorder suitable for logging the weight of a bird in a nest box or on a perch (ITE 728). To reduce the programme development time needed for this type of equipment, it was decided to upgrade the existing microprocessor (MOTOROLA) evaluation system to provide some of the facilities of a full development system, and this was achieved, at little extra cost, by linking the MOTOROLA system to the Bangor PDP-11 computer. The hardware now consists of a MOTOROLA MEK 6800D2 microprocessor board with extra memory, a VDU controller, ASCII keyboard, 2 EPROM programming boards, and an interface unit constructed to link the MEK board to a standard VDU computer port.

Microprocessor software has been written for the MEK system to allow communication with the PDP-11 computer and, in particular, to perform the following functions:

1. to make the MEK system operate as a computer terminal;
2. to allow transfer of microprocessor object code from a computer file directly into MEK memory;
3. to allow transfer of MEK memory bytes into a computer file;
4. to enable a computer-run program to control a digital cassette recorder connected into the MEK system.

With this new arrangement, programs can be written in assembly language from the MEK terminal, assembled on the computer, and fed back as object code into the MEK memory. As long as the program is assembled in 6800 code, it can either be run in the MEK system or transferred to EPROM for use in other microprocessor-based equipment. Programs for use with the RCA 1802 microprocessor can also be assembled this way, but the object code can only be stored in EPROM for use in a 1802 system.

As a result of this work, programming is now more efficient, less subject to error, and allows the full use of computer facilities for file handling, storage and editing.

C. R. Rafarel

Radio tracking

A number of projects at Banchory Research Station depend on the use of radio tracking equipment. A construction development programme is necessary to meet all the requirements (ITE 687), and quite frequent modifications have to be made at short notice to meet specific needs.

Some fresh tracking transmitters, including motion-sensor types, were field-tested on deer, badgers and grouse. Perhaps the most difficult problem encountered in telemetry work is how to keep the transmitters running for lengthy periods (often more than one year), and to provide strong useful signals under difficult field conditions, while at the same time preventing an increase in the weight of the pack. The electronics contribute only a small portion of the weight of a complete unit, the major part of which consists of the power source (usually primary cells). To overcome this difficulty, a start was made to construct a solar-powered transmitter for birds, using solar panels to charge a small (10/20/50 mAh) nickel-cadmium battery.

All the transmitters currently being built use discrete components. Studies have been started to consider the feasibility of a low-power miniature integrated circuit (CMOS), which will be able to control the transmitter and provide greater consistency for timing pulse duration and intervals. Sensor information would be conveyed by varying the integrated circuit timing periods.

J. A. Morris

Mist propagation studies

The propagation techniques and equipment at Bush were comprehensively examined during the year, following indications that overhead misting alone did not provide ideal conditions for rooting cuttings of, for example, *Picea sitchensis* and *Betula pendula*. Preliminary work suggested that high humidity in the cutting zone was more critical than wetness of leaf surface, and this humidity was achieved by (i) enclosing the mist bench in a polythene tent approximately 0·75 m high with closely fitting edges, (ii) reducing the water droplet size emitted by the jets by increasing the water pressure to 340–370 kPa, and (iii) adding 25% peat by volume to the root medium, which had previously been clean 3–4 mm grit. Temperatures in the mist bed were held at 20°C, with the glasshouse air temperature maintained within the range 15–30°C. Levels of light in the cutting zone were still adequate, even with a thin white emulsion spray on the glasshouse roof, a measure adopted to help keep the maximum temperatures in the mist tents to ∼30°C. These high temperatures were acceptable because relative humidity was maintained at 90–97%. Where possible, stock material was chosen for vigour and potted hardwood stockplants were 'coppiced' in March to produce vigorous young shoots. Once rooting had commenced in the mist benches, a liquid feed was given once a week. With the rooting conditions described, it was possible to get unusually large (30 cm) cuttings of *Betula pendula* to root in 15 days, providing in 6 months young clonal plants equal in size to 1 + 1 seedling 'whips'. The usual problem of variable rooting by different clones was not eliminated, but all rooting percentages were improved.

R. F. Ottley and F. J. Harvey

Culture Centre of Algae and Protozoa

GENERAL REVIEW

Preservation of genetic diversity

This objective, one of the priority aims of the World Conservation Strategy, referred to by the Director on page 13 of the ITE Annual Report for 1980 and again in this year's Report (p. 9), includes the 'preservation of as many varieties as possible of . . . microorganisms'. One of CCAP's main roles is to contribute to this aim, and the Centre currently maintains over 2000 cultures, representing about 400 genera and over 1000 species; about 60 have been added during the past year, including 2 unusual algae isolated by Professor S. J. Pirt of London University from fresh and brackish water, respectively, which grow at 30°C. Several new ciliates from local freshwater sources have been added to the collection of protozoa over the past year, and it is hoped to include some of the larger amoebae. Not all the maintained material is as fully characterized or as pure as one would wish, but the curators (J. P. Cann, Mrs E. A. Leeson and N. C. Pennick) and their colleagues are proceeding with the laborious task of remedying this defect as far as possible.

Maintenance of cultures by growth *in vitro* and serial subculture is not, of course, the best method of preserving the genome; cultivation introduces its own selection pressures, and the chance of mutations occurring is ever present. These problems can be virtually overcome by cryopreservation, and Mrs G. Coulson and Dr G. J. Morris are endeavouring to extend as far as possible the proportion of our stocks which can be successfully preserved in this way.

Distribution of cultures

Another of CCAP's main functions is the supply of cultures for teaching and research. Over 3500 such cultures were despatched during the 12 months ending 31 October 1981, to 25 countries (including Great Britain). Mrs A. Asher has analysed the data for the previous year (January–December 1980), with the following results: 4162 cultures were supplied in that year, 3095 to 78 British universities, 385 to 69 universities in 24 other countries, 152 to 33 schools in Britain, and 530 to other, mostly commercial, institutions throughout the world. In all, cultures were sent to 34 countries (including Britain), bringing in a gross revenue of about £12 000.

Research
The third major function of CCAP is research, largely morphological and taxonomic, into the Protista (unicellular algae and protozoa). Dr F. C. Page has made further progress in the application of electron microscopy to the taxonomy of amoebae. Although surface structure remains of special interest, the fine structure of the Golgi system has proved of value in some groups. Present work is concerned especially with larger and medium-sized amoebae requiring liquid media, but strains grown on agar, a culture method which has proved so valuable for many diverse amoebae, are still being studied. Examination of ultra-thin sections, chromium-shadowing, and scanning electron microscopy are being applied to the study of complex scales on *Mayorella* and *Cochliopodium.* These are the principal genera possessing true scales, as distinguished from certain more delicate, adhesive structures. The scales of *Mayorella* are boat-shaped and biradially symmetrical, covering the entire surface of the amoeba. Those of *Cochliopodium* are tall, radially symmetrical structures, constituting a tectum which covers only the free surface (that not applied to the substratum in locomotion). The scales of *Mayorella* cannot be detected by light microscopy, and it has only recently been found that some *Mayorella*-like organisms have a different sort of surface coat. These species differ somewhat from true, scale-bearing *Mayorella*, the structure of their Golgi apparatus being strikingly different. Although the structures of *Cochliopodium* scales, like that of *Mayorella* scales, cannot be studied with the light microscope, the scales of *Cochliopodium* are visible as a fine punctuation on many species, and the tectum as a whole can be demonstrated with light-microscopical techniques. In both genera, the scales appear to be entirely organic, although the chemical constitution is not known beyond the fact that it includes polysaccharide. *Mayorella* is always considered a member of the Gymnamoebia (naked lobose amoebae), while most workers consider *Cochliopodium* a testacean (shelled amoeba), with its tectum corresponding to the rest of other testaceans. As the detailed structure of the scales differs amongst the species in each genus, this character appears promising for species distinction. *Mayorella is* widespread in both fresh and salt water. *Cochliopodium* occurs in both those environments, but is also common in terrestrial habitats and is often reported in ecological studies. 1981 saw the publication by ITE of Dr Page's book 'The culture and use of free-living protozoa in teaching'. This book, referred to in last year's Annual Report (p. 117), originated from the recognition of problems in secondary and higher education in developing countries, and is intended to make possible the maintenance of small collections of protozoa for teaching where circumstances make it impractical to order cultures. Methods are described enabling these organisms to be maintained and used for demonstrating biological principles with a minimum of equipment, by teachers with little previous experience of protozoa.

Drs Hilary Belcher and Erica Swale have continued their ecological and taxonomic study of freshwater algae, in the river Thames and elsewhere, including, unlikely though it may sound, the roof of the Culture Centre itself. This roof is flat, with plastic domed rooflights, and the heat of the sun has caused these to sag, forming 3 hollows which hold rain water. The largest of these is deep and persistent enough for starlings to bathe in during dry weather, and their flapping and splashing attracted attention to the water itself. When sampled, it was found to be deep green in colour, due to a dense growth of the beautiful colonial alga *Stephanosphaera* (Figure 52). The usual habitat of this alga is rain-filled hollows in rocks such as carboniferous limestone, of which Cambridgeshire and its surrounding counties are singularly devoid. Encouraged by this observation, the gutters were also examined, as they too contained several persistent puddles. A bright green flocculent mass in one of these proved to be desmids belonging to 2 species, the not uncommon *Actinotaenium curtum* and the rare and elegant *Staurastrum polonicum*. Neither the *Stephanosphaera* colonies nor the ordinary desmid cells can withstand

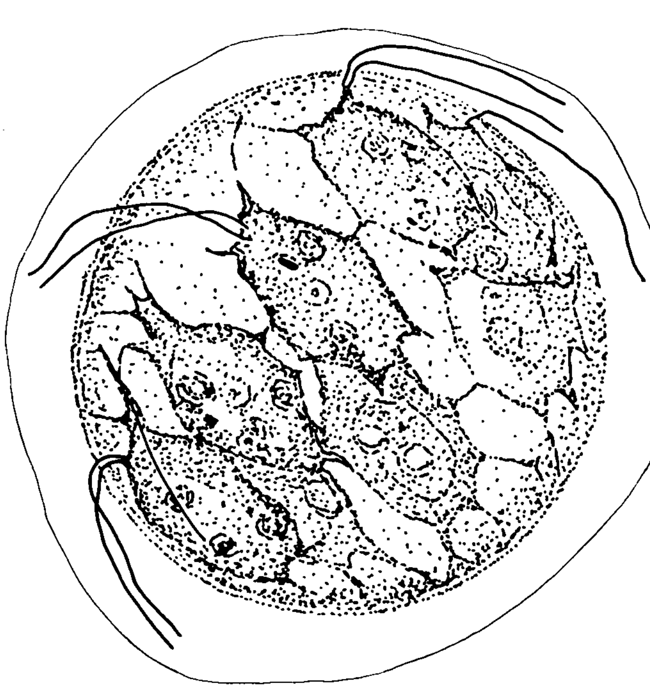

Figure 52 Colony of the green alga Stephanosphaera, *as found growing on the roof of the Culture Centre of Algae and Protozoa, Cambridge; the colonies are up to 60 µm in diameter. Drawing by E Swale, from 'A beginner's guide to freshwater algae', by H Belcher and E Swale, 1976. London: HMSO.*

desiccation, but all form resistant zygotes, and they probably arrived on the roof in this state, perhaps carried by birds for over 100 miles. A search is being made for similar rooftop puddles on other buildings. Drs Belcher and Swale have prepared a booklet describing simple methods of cultivating free-living protozoa, complementary to that by Dr Page (see above), which awaits the availability of funds for its publication, and are also writing an illustrated guide to diatoms to supplement their 2 very successful earlier ITE publications on freshwater algae and river phytoplankton.

Dr D. J. Hibberd has completed an investigation of the cytology and ultra-structure of the marine colonial amoeboid alga *Chorarchnion reptans* Geitler. Both amoeboid and flagellate stages of this organism have a unique combination of structural features. Although joint work with Professor N. Withers (University of Hawaii) has shown that *C. reptans* contains both chlorophyll *a* and chlorophyll *b*, on the basis of ultrastructural characters it is clearly phylogenetically remote from all green plants. Its chloroplasts were therefore probably acquired originally by symbiosis with a green eukaryotic alga. The presence of a ribosome-containing cytoplasmic compartment around the chloroplast, only otherwise known in members of the Cryptophyceae, possibly represents a remnant of the cytoplasm of the reduced symbiont. Taxonomically, *C. reptans* is to form the basis of a new class and division of algae.

A joint project between Dr Hibberd, Dr J. C. Green (Marine Biological Association, Plymouth) and Professor R. N. Pienaar (University of Natal) on the taxonomy of the genus *Prymnesium* has been completed. Species of *Prymnesium* are economically important as the causative agents of mass fish mortalities in brackish water. Although the ultrastructure and biochemistry of one species, *P. parvum*, is well-known, the taxonomy of the genus is confused. Examination of the structure and arrangement of the scales of several strains, including new isolates from North America, Britain and South Africa, has resulted in the description of one new species, a redescription of *P. parvum*, and a re-assessment of the taxonomy of the genus as a whole, which has provided a basis for its separation from the closely related genus *Chrysochromulina*.

Dr Hans Preisig's 2-year visit to CCAP ended in December of this year. He has undertaken most fruitful collaboration with Dr Hibberd and will be sadly missed (both personally and scientifically) on his return to Zurich. After spending his first year learning from K. J. Clarke the techniques of electron microscopy, Dr Preisig applied this knowledge to investigating the ultrastructure of various phytoflagellates, especially the little-known colourless scale-bearing genus *Paraphysomonas* (Chrysophyceae), of which many known and new species have been found in the Cambridge area. The taxonomic results, based mainly on scale ultrastructure, are being presented in 2 joint publications with Dr Hibberd, in which 30 species, 16 of them new, will be described. In addition, 2 species of the pigmented chrysophycean genera *Spiniferomonas* and *Lepidochromonas* will be included within *Paraphysomonas*. The type species of *Spiniferomonas* and the only known species of *Lepidochromonas* were found to lack chloroplasts and to possess taxonomic features also found in *Paraphysomonas*. This conclusion necessitated the establishment of a new generic name for the remaining species of *Spiniferomonas* containing a chloroplast. The results of the investigations on internal ultrastructure of these Chrysophyceae will be given in a third paper.

Fundamental research on cryobiology is continuing: apart from its basic scientific value, it is hoped that further understanding of the processes involved in cellular freezing injury will lead to the possibility of its mitigation, and thus extend the range of protistan strains which can be cryopreserved, with the advantages outlined above. Mrs Coulson and Dr Morris are studying the biochemistry of freezing injury using a mutant of *Chlamydomonas reinhardii* which lacks a cell wall, with emphasis on alterations in the membrane lipid composition following freezing and thawing and the potentially damaging effects of gas bubble formation during freezing. Study of freeze-fractured and freeze-etched specimens of 3 'standard' model organisms (*C. reinhardii, Tetrahymena* and *Euglena*) by scanning and transmission electron microscopy (Dr Morris, Mrs Coulson and K. J. Clarke) is providing further information on freezing damage. Dr Morris's book on 'Cryopreservation' was published by ITE during the year.

In addition to this work and to collaborating in the morphological studies of other staff members, K. J. Clarke is working jointly with Dr David Morris of the British Antarctic Survey (BAS) on the ultrastructure of krill feeding apparatus, as part of the project on the importance of algae and protozoa to plankton feeders in the food-chains of antarctic waters.

In addition to their time-consuming work as curators, Mrs Leeson, J. P. Cann and N. C. Pennick are also undertaking research. Mrs Leeson has begun a study of biochemical mechanisms involved in the temperature limits of growth for *Chlamydomonas*, a topic obviously related to Dr Morris's work. Two species, *C. yellowstoniensis* and *C. nivalis*, both isolated from snow, were obtained from the University of Texas for comparative studies with CCAP's strain of *C. nivalis* and the chilling-sensitive species *C. reinhardii*. It is hoped that more isolates will be obtained by the British Antarctic Survey expedition in early 1982. Mrs Leeson is determining growth patterns of the strains between 0° and 30°C, and attempting to find suitable assays for monitoring temperature-induced metabolic changes. Partial success has been achieved using the tetrazolium salt assay, in which 2,3,5 triphenyltetrazolium chloride is converted to formazan, and the uptake of rubidium chloride will be studied. It is intended to measure temperature-induced changes in membrane fluidity of naked protoplasts. *C. reinhardii* produces naked gametes by secreting a wall-dissolving substance, which could be extracted and used to dissolve walls of vegetative cells. As a preliminary, Mrs Leeson is studying sexual reproduction of *C. nivalis* and *C. yellowstoniensis* by light and electron microscopy.

J. P. Cann, in collaboration with Dr Page, has completed a study of taxonomy and classification of the genus *Paramoeba*, and is currently comparing the ultrastructure of strains of *Leptomyxa* in the collection in order to gain more information on their taxonomic position. N. C. Pennick and K. J. Clarke are winding up a lengthy study of the Prasinophyceae and other small unicellular algae, which has led to the publication of some 17 papers in the course of the past 9 years, with several others in press (see Figure 53). They are continuing work on the surface structure of Cryptomonadaceae. It is hoped that the taxonomic work will be extended into 'molecular taxonomy', involving characterization of RNA, DNA, polypeptides and isoenzymes, in collaboration with the London School of Hygiene and Tropical Medicine (LSHTM) and the Molteno Institute, Cambridge.

These 'molecular' techniques, as well as conventional morphology, are being used by Mr Pennick and Dr Baker in the characterization of various Trypanosomatidae; they are also collaborating with Dr M. J. Turner and others at the Molteno Institute in work involving hybridization of 'cloned' trypanosomal DNA. Polypeptide analysis of several strains of trypanosomes (subgenus *Schizotrypanum*, isolated from bats), using the 'fingerprinting' technique of electrophoresis in SDS-PAGE gels, largely substantiated taxonomic groupings already deduced from DNA and isoenzyme analyses and conventional morphology, while suggesting one, possibly new, infraspecific taxon amongst stocks originating from South America. The work has been accepted for publication in 'Systematic Parasitology', under the senior authorship of Dr Angela E. R. Taylor (LSHTM). Preliminary results of an investigation by Dr Robert Kenward (Monks Wood) and Dr Baker, into the epidemiology of a blood parasite of squirrels, are described elsewhere in this Report (pp. 105-106).

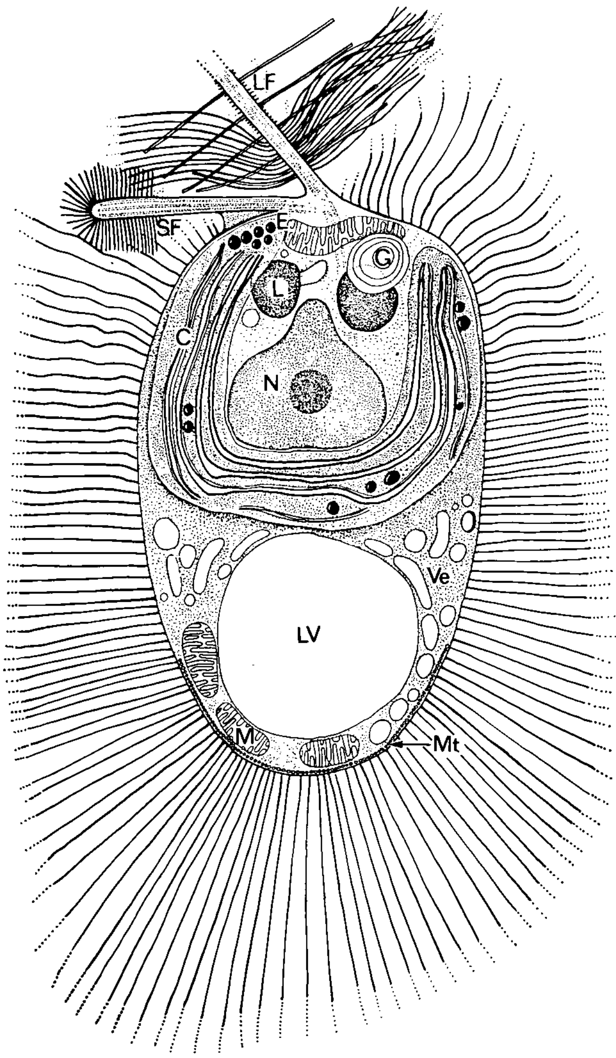

Figure 53 Diagram of the internal structure, revealed by electron microscopy, of a new species of the unicellular alga Ochromonas *(description in press); Culture Centre of Algae and Protozoa strain 933/25. Drawn by N C Pennick from electron micrographs by K J Clarke and N C Pennick. The cell is about 4 µm long. E = eyespot; LF = long flagellum; LV = leucosin vacuole; M = mitochondrion; Mt = mictrotubule; N = nucleus; SF = short flagellum; Ve = vesicle; L = leucosin; C = chloroplast; G = Golgi apparatus.*

We were delighted to welcome during the year Dr Lydia Kalinina, from the Institute of Cytology in Leningrad, for an all-too-short 3 weeks' visit, arranged under the exchange scheme sponsored jointly by the Royal Society of London and the Academy of Sciences of the USSR. Dr Kalinina's visit gave Dr Page the opportunity to examine some of the many Russian isolates of *Amoeba proteus*, and a collaborative taxonomic study of one isolate is under way, combining morphological (including ultrastructural) and physiological approaches. These larger amoebae are used in many cell biological investigations and, although it is recognized that some of the isolates used are not *A. proteus*, few have been identified or validly described as new species. Classification of their taxonomy is therefore much needed. Dr Kalinina also worked with Dr Morris (and Dr C. Polge at the Agricultural Research Council Institute of Animal Physiology in Cambridge) on aspects of the cryobiology of *A. proteus*. The amoeba is damaged by chilling *per se*: even short periods of exposure to −10°C, in the absence of ice, resulted in an 85% loss of viability. This is an unusual response for animal cells, which has many similarities to chilling injury in tropical plants. Initial studies suggested that it may have been due to depolymerization of the cytoskeletal structure at low temperature.

Other visiting workers included Ms S. Wehnert (University of Guelph, Canada) and 2 'sandwich' students – T. Paul (Brunel University) and M. McLellan (Hatfield Polytechnic).

The library has been fully integrated into the ITE system. Mrs A. Asher, greatly helped by D. Spalding from ITE headquarters, is computerizing all the strain data both for record purposes and to aid in the production of a new list of strains.

J. R. Baker

A PROTOZOAN BLOOD PARASITE OF SQUIRRELS

The haemogregarines are a rather heterogeneous group of parasitic protozoa belonging to the phylum Apicomplexa (more traditionally known as Sporozoa). At one stage of their life cycle, they inhabit the blood cells of vertebrates; some also live in fixed tissue cells, and all are transmitted from vertebrate to vertebrate by an invertebrate vector – usually a leech or insect. 'True' haemogregarines (of the suborder Adeleina) have been reported from a range of rodents, but not other mammals, in Britain; the so-called 'haemogregarines' of British birds belong to a different suborder (Eimeriina), which really should not be referred to by that name (Cox 1970; Baker 1974). As a group, adeleine haemogregarines have been relatively little studied, and there is no evidence that any species is acutely harmful to its host. Nevertheless, the presence of the parasites might conceivably be harmful under conditions of abnormal stress. Alternatively, they might exert a depressive effect on the host's ability to defend itself immunologically against other infections; several instances of immunodepression by protozoan and other parasites of man and domestic animals have been revealed during the last decade or so (Ogilvie & Wilson 1976), and the phenomenon is probably more widespread than is presently recognized.

Coles (1914) recorded, and briefly described, a haemogregarine in the white blood cells (leucocytes) of an 'English squirrel' (presumably *Sciurus vulgaris*) caught near Reading in Berkshire. He named the parasite *Haemogregarina sciuri* (Plate 14). It was subsequently rediscovered by Dasgupta and Medeeniya (1958) in both *S. vulgaris* and *S. carolinensis*, and transferred to the genus *Hepatozoon*; developmental stages were reported in the flea *Orchopeas wickhami*. No further study of the parasite appears to have been made, so it seemed worthwhile to take advantage of the opportunity to examine blood films provided by the regular sampling of several populations of *S. carolinensis* which was already in progress (pp. 15 – 18).

Material and methods

Squirrels (*Sciurus carolinensis*) were live-trapped on 29 June and 9 July 1981, at the following locations (identified in Table 39 by the initial letters given in parentheses below).

Pitsford Reservoir (P), National Grid reference SP 770695;
Salcey Forest (S), SP 800 510;
Woburn Park (W), SP 970 340;
Elton Park (E), TL 085 925;
Monks Wood and Bevill's Wood (B), TL 200 800.
All locations lie within the English counties of Cambridgeshire, Bedfordshire, Northamptonshire and Buckinghamshire, approximately longitude 0° 30' W and latitude 52° 30' N.

Table 39. Prevalence of infection with *H. sciuri* in male and female squirrels at different sites.

Site	Number infected/number examined	
	Female	Male
P	1/3	5/6
S	3/8	12/16
W	3/14	9/17
E	14/30	20/28
B	–	4/4
Total	21/55	50/71

Squirrels were classed as juvenile (up to about 4-months old), sub-adult (1 – 1½ years) and adult (2 years or older). Average body weights for the groups were: male juvenile, 384 g; male sub-adult, 476 g; male adult, 514 g; female juvenile, 391 g; female sub-adult, 490 g; female adult, 536 g. Most of the animals were collected in areas from which squirrels were to be removed; they were killed by an intracranial captive bolt shot, and blood was collected from the wound. A few animals, from areas where the population was not to be reduced, were bled from the tail tip.

Thick and thin blood films were made and air-dried. After fixing the thin films with methanol, both were treated with Giemsa's stain and examined microscopically at a magnification of × 780. The intensity of parasitaemia was arbitrarily scored as 'light', 'average', or 'heavy'.

Results

A total of 126 animals (55 females and 71 males) was examined; *H. sciuri* was seen in the blood of 71 (56%), comprising 21 females (38%) and 50 males (70%) (Table 39). The difference in infection rates between sexes was not significant within any area, though males were more commonly infected in all areas; it was, however, highly significant when all groups and areas were combined (sign test, $P = 0{\cdot}004$). The differences between sites were not great, and may have been due only to sampling error.

Table 40 shows the sex and age distribution of hosts according to intensity of parasitaemia. The proportion of infected animals was highest among sub-adults, and lowest among juveniles, in both sexes; a site-by-age non-parametric analysis of variance showed this difference to be statistically significant ($P<0{\cdot}001$).

Table 40. Intensity of infection with *H. sciuri* in squirrels grouped according to age and sex.

			Parasitaemia		
Sex	Age	Negative	Light	Average	Heavy
Male	Juvenile	9	1	1	1
	Sub-adult	2	5	14	5
	Adult	10	4	12	7
	Total	21	10	27	13
Female	Juvenile	14	0	0	0
	Sub-adult	5	5	8	1
	Adult	13	1	3	3
	Total	32	6	11	4
Both	Total	53	16	38	17

Discussion

The difference in infection rate according to age could result from juveniles either having not yet become infected or being within the prepatent period of infection, and some adults having recovered from infection and (presumably) become immune to reinfection. Alternatively, it could reflect a difference in transmission rate between successive years, with 1981 (when the juveniles were born) having particularly low, and 1980 particularly high, transmission rates. *H. sciuri* is probably transmitted by the flea *Orchopeas wickhami* (Dasgupta & Medeeniya 1958), so that exposure to infected vectors could presumably occur early, in the drey. It seems unlikely that the prepatent period of infection would be more than one month. However, as pregnant females build new dreys into which they move before giving birth, it is possible that they, and the new-born young, are not immediately exposed, or are less exposed, to the bite of infected fleas, which could perhaps account, at least in part, for the observed difference in infection rate between males and females, as well as for the low rate in juveniles of both sexes (3/26; 11·5%) compared with sub-adults (38/46; 82·6%) and adults (30/54; 55·6%). It is also conceivable that flea populations, and hence transmission intensity, could vary from year to year, being influenced by, perhaps, the severity of the preceding winter. Further speculation is probably fruitless without extra observation.

J. R. Baker and R. E. Kenward

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Acknowledgement

We are very grateful to Jane Oliver for help with the trapping.

Projects

listed by Subdivisions as at 11th February 1982

The listing by Subdivisions also shows the number of the Station at which the Project Leader is located:

1 Monks Wood
2 Merlewood
3 c/o University of East Anglia, Norwich
4 Furzebrook
5 Edinburgh, Bush
6 Edinburgh, Craighall Road
7 Banchory
9 Bangor
10 Hills Road, Cambridge
12 CCAP, Cambridge

Key for symbols used against project number:

@ Nature Conservancy Council contract
\+ Department of Environment contract
£ Other outside contract
! PhD or other student project
$ Visiting worker project

VERTEBRATE ECOLOGY SUBDIVISION

			Code
54	Red deer ecology on Rhum	V. P. W. Lowe	2
59	Taxonomy of the red squirrel	V. P. W. Lowe	2
67	Prey selection in redshank	J. D. Goss-Custard	4
104	Distribution and segregation of red deer	B. W. Staines	7
111	Population dynamics of red deer at Glen Feshie	B. Mitchell	7
116	Freshwater survey of Shetland	P. S. Maitland	6
117@	Freshwater survey of Great Britain	P. S. Maitland	6
123	Zoobenthos at Loch Leven	P. S. Maitland	6
124	Distribution & biology of fish in Great Britain	P. S. Maitland	6
136	Hen harrier study in Orkney	N. Picozzi	7
159	Upland bird project	D. C. Seel	9
209@	Vertebrate recording schemes	H. Arnold	1
291@	Population ecology of bats	R. E. Stebbings	1
292@	Specialist advice on bats	R. E. Stebbings	1
363	Dispersion of field voles in Scotland	W. N. Charles	6
386	Behaviour and dispersion of badgers	H. Kruuk	7
391	British mammals — the red fox	V. P. W. Lowe	2
441	Oystercatcher & shellfish interaction	J. D. Goss-Custard	4
442	Ecology of capercaillie	R. Moss	7
461@	Puffins and pollutants	M. P. Harris	7
479	Red deer in production forests	B. W. Staines	7
499	Classification of Cervidae	V. P. W. Lowe	2
524	Fluoride in predatory mammals	K. C. Walton	9
525	Fluoride in predatory birds	D. C. Seel	9
528	Red deer populations in woodland habitats	B. Mitchell	7
543!	Population ecology of the red squirrel	V. P. W. Lowe	2
619	Small rodents in a Sitka spruce plantation	A. G. Thomson	9
636	Song bird density & woodland diversity	D. Jenkins	7
638	Monitoring otters at Dinnet	D. Jenkins	7
676	Ecology of lampreys in Loch Lomond	P. S. Maitland	6
687	Radio location & telemetry development	T. Parish	7
705£	Impact of barytes mine project	P. S. Maitland	6
715£	Shetland otters	D. Jenkins	7
730	Analysis of coastal otter faeces in Scotland	D. Jenkins	7
733	Plant fragments in diets of upland herbivores	W. N. Charles	6
734	Estimation of seabird numbers	M. P. Harris	7
735	Oystercatcher population dynamics	M. P. Harris	7
751	National survey of fluoride in predatory birds	D. C. Seel	9
753	Fluoride and magpies	D. C. Seel	9
764£	Habitat requirements of black grouse	N. Picozzi	7
765	Ecology of the heron	M. Marquiss	6

INVERTEBRATE ECOLOGY SUBDIVISION

65	Invertebrate population studies	S. McGrorty	4
185	Effect of urbanisation	B. N. K. Davis	1
188	Woodland invertebrates	R. C. Welch	1
202	The Roman snail	E. Pollard	1
204@	Assessing butterfly abundance	E. Pollard	1
211@	Lepidoptera distribution maps scheme	J. Heath	1
223	European invertebrate survey	J. Heath	1
230	Grassland management — invertebrates	M. G. Morris	4
232	Butterfly studies at Porton Range	M. G. Morris	4
236	Invertebrate populations in grass sward	E. Duffey	1

241	The fauna of box	L. K. Ward	4
243	Scrub succession at Aston Rowant NNR	L. K. Ward	4
255	Ecology of *Myrmica* species	G. W. Elmes	4
256	Protein electrophoresis	B. Pearson	4
262	Digestive enzymes	A. Abbott	4
270	Distributional studies on spiders	P. Merrett	4
274	Physiology of soil fauna	N. R. Webb	4
295	Survey of juniper in N. England	L. K. Ward	4
296	Scrub management at Castor Hanglands	L. K. Ward	4
309	Phytophagous insects data bank	L. K. Ward	4
345	Spiders in East Anglian fens	E. Duffey	1
400	The large blue butterfly	J. A. Thomas	4
403	The black hairstreak butterfly	J. A. Thomas	4
404	The brown hairstreak butterfly	J. A. Thomas	4
405	Fauna of pasture woodlands	P. T. Harding	1
406	Distrib and ecology of non-marine Isopoda	P. T. Harding	1
407	British Staphylinidae (Coleoptera)	R. C. Welch	1
414	Hartland Moor spider survey	P. Merrett	4
469	Scottish invertebrate survey	R. C. Welch	1
470	Upland invertebrates	A. Buse	9
500	Recolonization by spiders on Hartland Moor	P. Merrett	4
509	Wood white butterfly population ecology	E. Pollard	1
527	Long-term changes in zooplankton	D. H. Jones	6
547	Study of the genus *Micropteryx*	J. Heath	1
557@	Terrestrial and freshwater invertebrate surveys	P. T. Harding	1
568	Subcortical fauna in oak	M. G. Yates	1
569	Insect fauna of *Helianthemum* and *Genista*	B. N. K. Davis	1
570	Studies on fritillary butterflies	E. Pollard	1
577	Predation of freshwater zooplankton	D. H. Jones	6
592	Spatial organisation of zooplankton populations	(Suspended)	6
615	Fragmentation of heaths and invertebrates	N. R. Webb	4
628!	Colonization of limestone quarries	D. Park	1
641	Invertebrate fauna of *Nothofagus* and *Quercus*	R. C. Welch	1
644	Breeding success & survival in the common toad	C. J. Reading	4
656@	Marine invertebrate recording schemes	H. Arnold	1
657	Biological Records Centre — general	J. Heath	1
660	Simultaneous butterfly population studies	J. A. Thomas	4
686	Aerial dispersal in spiders at Minworth	E. Duffey	1
689	Insect fauna of the stinging nettle	B. N. K. Davis	1
690	Plant succession in a limestone quarry	B. N. K. Davis	1
691	Urban climate and invertebrate ecology	B. N. K. Davis	1
694	Zooplankton communities in freshwater lakes	D. H. Jones	6
708!	Structure of spider communities on heathland	P. J. Hopkins	4
709	Techniques for rearing the large blue butterfly	J. C. Wardlaw	4
722	The habitat ecology of the spider *Eresus niger*	P. Merrett	4
737	Populn genetics of *Pardosa monticola* spiders	R. G. Snazell	4
757	Ecology of *Myrmica* populations in Nepal, 1981	G. W. Elmes	4

ANIMAL FUNCTION SUBDIVISION

137	Sparrowhawk ecology	I. Newton	1
181@	Birds of prey and pollution	A. A. Bell	1
193	Stone curlew and lapwing	N. J. Westwood	1
199	Avian reproduction and pollutants	S. Dobson	1
289	Residues and effects of pollutants	F. Moriarty	1
413	Breeding biology of the cuckoo	I. Wyllie	1
444	Endocrine lesions in birds	S. Dobson	1
455	Heavy metals in avian species	D. Osborn	1
559	Ecophysiology of the rabbit	D. T. Davies	1
606	Grey squirrel damage and management	R. E. Kenward	1
630	Stress in birds	A. Dawson	1

692	Goshawk population dynamics	R. E. Kenward	1
728	Kestrels in farmland	A. Village	1
739	Life history of the common frog	C. P. Cummins	1

GROUSE AND MOORLAND ECOLOGY

129	Red grouse and ptarmigan populations	A. Watson	7
130	Management of grouse and moorlands	A. Watson	7
131	Golden plover populations	A. Watson	7
132	Monitoring in the Cairngorms	A. Watson	7

HEATHLAND SOCIAL INSECTS

252	Hartland Moor NNR survey	M. V. Brian	4
253	*Tetramorium caespitum* populations	M. V. Brian	4
258	Degree of control by queen ants	M. V. Brian	4
370	Experimental reduction of inter-species competition in ants	M. V. Brian	4
371!	Regulation of sexual production in *Myrmica*	E. J. M. Evesham	4

PLANT BIOLOGY SUBDIVISION

2	Meteorological factors in classification	E. J. White	5
82	Seed produced by montane plants	G. R. Miller	7
102	Mountain vegetation populations	N. G. Bayfield	7
158	Community processes (physiology)	D. F. Perkins	9
160	Fluorine pollution studies	D. F. Perkins	9
208@	Botanical data bank	C. D. Preston	1
246	Physical environment, forest structure	E. D. Ford	5
265	Regeneration on lowland heaths	S. B. Chapman	4
266	Root dynamics of *Calluna vulgaris*	S. B. Chapman	4
269	Autecology of *Gentiana pneumonanthe*	S. B. Chapman	4
346	Genecology of grass species	A. J. Gray	4
359	Fibre yield of poplar coppice	M. G. R. Cannell	5
410	Tundra plants (bryophytes)	T. V. Callaghan	2
411	Taxonomy of bryophytes		5
451	Analysis of S. Georgian graminoids	T. V. Callaghan	2
575	Regeneration & growth of bracken rhizomes	R. E. Daniels	4
576	Genecological variation in *Sphagnum*	R. E. Daniels	4
648	Highcliffe stabilization trials	A. J. Gray	4
649	Demographic genetics of *Agrostis setacea*	A. J. Gray	4
674£	Plant species for energy in Great Britain	T. V. Callaghan	2
702	Selection of frost-hardy trees	M. G. R. Cannell	5
720	Fruitbodies of mycorrhizal fungi	J. Wilson	5
721	Dry matter in forests: world review	M. G. R. Cannell	5
750	Domestication of tropical hardwoods	R. R. B. Leakey	5
767	Formation of cones by lodgepole pine	K. A. Longman	5
770	Evaluation of conifer clones and progenies	M. G. R. Cannell	5
773	Silviculture of respacing Sitka spruce	E. D. Ford	5

PLANT COMMUNITY ECOLOGY SUBDIVISION

1	Semi-natural woodland classification	R. G. H. Bunce	2
9	Monitoring at Stonechest	J. M. Sykes	2
14	Tree girth changes in 5 NNR's	A. D. Horrill	2
55	Establishment of trees at Moor House	A. H. F. Brown	2
75	Control of *Spartina*	D. G. Hewett	9
77	Cliff vegetation methods	D. G. Hewett	9
78	Management of sand dunes in Wales	D. G. Hewett	9
92	Grazing intensities causing change	D. Welch	7
93	Assessing animal usage in N.E. Scotland	D. Welch	7

95	Importance of dung for botany change	D. Welch	7
163	Ordination and classification methods	M. O. Hill	9
165	N. Wales bryophyte recording	M. O. Hill	9
225	Population studies on orchids	T. C. E. Wells	1
227	Sheep grazing on chalk grass flora	T. C. E. Wells	1
228	Effect of cutting on chalk grassland	T. C. E. Wells	1
242@	Establishment of herb-rich swards	T. C. E. Wells	1
340	Survey of Scottish coasts	D. S. Ranwell	3
360£	Trees on industrial spoil	J. E. Good	9
367	The Gisburn experiment	A. H. F. Brown	2
374	Sand dune ecology in East Anglia	L. A. Boorman	1
377	Environmental perception studies	J. Sheail	1
380+	Monitoring of atmospheric SO_2	I. A. Nicholson	7
381	Plankton populations at Loch Leven	(Suspended)	6
389	Management effect in lowland coppices	A. H. F. Brown	2
424	Ecological survey of Britain	R. G. H. Bunce	2
426	Modelling of sulphur pollution	I. A. Nicholson	7
452+	Foliar leaching and acid rain	J. W. Kinnaird	7
453	SO_2 dry deposition in Scots pine forest	I. A. Nicholson	7
454	NCC monitoring of woodlands	J. M. Sykes	2
463	Age class of amenity trees	J. E. Good	9
466@	Ecology of railway land	C. M. Sargent	1
467	Roadside experiments	C. M. Sargent	1
483	Scottish deciduous woodlands	R. G. H. Bunce	2
539	Phragmites "dieback" — Norfolk Broads	L. A. Boorman	1
549@	Monitoring in native pinewoods	J. M. Sykes	2
567+	Coastal dune management guide	D. S. Ranwell	3
573+	Amenity grass — stage 2	M. D. Hooper	1
584	Nutrient loading, phytoplankton & eutrophication	A. E. Bailey-Watts	6
585	Diatom ecology	A. E. Bailey-Watts	6
586	Freshwater phytoplankton periodicity	A. E. Bailey-Watts	6
599@	Bracken and scrub control on lowland heaths	R. H. Marrs	1
602	Modelling sports turf wear	T. W. Parr	1
625	Effects of clear felling in upland forests	M. O. Hill	9
626	Welsh wetlands survey	D. F. Evans	9
633	Water level & vegetation change — Kirkconnell Flow	J. M. Sykes	2
634	Field plot survey — Monks Wood	T. C. E. Wells	1
650	Amenity grass irrigation	M. D. Hooper	1
665	Coastal management	D. S. Ranwell	3
666	Coastal publications	D. S. Ranwell	3
669	Interaction of grazing and air pollution	J. W. Ashenden	9
683	Monks Wood symposia — area and isolation	M. D. Hooper	1
684£	Mapping Broadland vegetation with aerial photos	R. M. Fuller	1
697	History of pollution and pesticides	J. Sheail	1
711	Tree growth and climate	A. Millar	2
726	Restoration of heathland vegetation	R. H. Marrs	1
740	Spatial data symposium	R. M. Fuller	1
743	Railway resource monitoring	C. M. Sargent	1
744	Effects of grazing in Snowdonia	M. O. Hill	9
745£	Land availability for wood energy plantations	R. G. H. Bunce	2
746	Grazing in woodlands	T. W. Ashenden	9

SOIL SCIENCE SUBDIVISION

4	Soil classificâtion methods	P. J. A. Howard	2
17	Meathop Wood IBP study	J. E. Satchell	2
39	Phosphorus turnover in soils	A. F. Harrison	2
61	Variation in growth of birch and sycamore	A. F. Harrison	2
88	Plant establishment in shrubs	J. Miles	7
89	*Calluna-Molinia-Trichophorum* management	J. Miles	7
90	Birch on moorland soil and vegetation	J. Miles	7

148	Soil erosion on Farne Islands	M. Hornung	9
153	Mineralogical methods	A. Hatton	9
245	Genetics of *Betula* nutrition	J. Pelham	5
358	Earthworm production in organic waste	J. E. Satchell	2
364	Early growth of trees	A. F. Harrison	2
398	Upland land use	O. W. Heal	2
431	Soil change through afforestation	P. J. A. Howard	2
432	Effect of birch litter on earthworms	J. E. Satchell	2
438	Ecology of *Mycena galopus*	J. C. Frankland	2
471	Soils of Upper Teesdale	M. Hornung	9
522	Ecology of vegetation change in uplands	D. F. Ball	9
533	Podzolic soils	P. A. Stevens	9
534	National land characterisation	D. F. Ball	9
541	Marginal land in Cumbria	C. B. Benefield	2
551	Overseas liaison activities	J. E. Satchell	2
554	Cumbria land classes and soil types	J. K. Adamson	2
561	Soil fertility	M. Hornung	9
589	Microbial characteristics in soil	P. M. Latter	2
594	Geochemical cycling	M. Hornung	9
654	Status of mycorrhizas in soil	J. Dighton	2
673	Nutrient transfer efficiency of mycorrhizas	J. Dighton	2
712	Organic matter quality and tree growth	O. W. Heal	2
714	Role of forest vegetation in pedogenesis	P. J. A. Howard	2
755$	Microfungal community structure in forests	P. Widden	2

DATA AND INFORMATION SUBDIVISION

216	Register of NNRs	G. L. Radford	9
306	Statistical analysis of spatial patterns	P. Rothery	10
307	Index of eggshell thickness	P. H. Cryer	10
308	Data from multi-compartment systems	P. H. Cryer	10
365	Competition between grass species	H. E. Jones	2
376	Statistical training	C. Milner	9
402	Biometrics advice to NERC	M. D. Mountford	10
434	ITE computing services	C. Milner	9
457	Grazing models	C. Milner	9
512	National collection of birch	A. S. Gardiner	2
514	British birch publication	A. S. Gardiner	2
529	Biological data bank	D. M. Greene	1
531	Statistical and computing advice, Furzebrook	R. T. Clarke	4
556	Estimation in acid rain	K. H. Lakhani	1
564	British Hydracarina — mainly of mosses	N. Hamilton	2
565	Bibliography of Shetland	N. Hamilton	2
566	Islands: biogeographic analysis	N. Hamilton	2
574	Potential for fuel cropping in upland Wales	D. I. Thomas	9
591	Terrestrial Environment Information System	B. Wyatt	9
609+	Biological classification of UK rivers	D. Moss	9
612	Analysis of common birds census	M. D. Mountford	10
613	Computerization of ITE/NERC costing procedure	M. D. Mountford	10
614	Numerical classification	M. D. Mountford	10
621	Models of rabies epidemiology	P. J. Bacon	2
622	Applications of systems analysis	P. J. Bacon	2
623	Entity, attribute, relationship of data bases	P. J. Bacon	2
624	Population genetics	P. J. Bacon	2
642	Physics of freshwater systems	I. R. Smith	6
645	Effects of soil chemistry on decomposition	D. D. French	7
646	Statistical consultancy service at Bangor	D. Moss	9
647	Dipper territory and population models	D. Moss	9
663	Estimation of abundance of populations	M. D. Mountford	10
664	Computing/statistical service at Banchory	D. D. French	7
668	Biometrical consultancy	M. D. Mountford	10

670	Statistical advice & computing at Edinburgh	R. I. Smith	5
671	Analysis of BRC data	G. L. Radford	9
672	Computing facilities at Bangor	G. L. Radford	9
699	Checklist of computer programs	D. K. Lindley	2
700 +	Ecological guidelines for locational strategies	G. L. Radford	9
717	Birch variation and environmental differences	A. S. Gardiner	2
732@	NCR site information system	G. L. Radford	9
760£	EEC ecological mapping	B. K. Wyatt	9

CHEMISTRY AND INSTRUMENTATION SUBDIVISION

52	Biological studies of *Glomeris*	K. L. Bocock	2
62	National plant nutrient survey	H. M. Grimshaw	2
378	Chemical data bank	S. E. Allen	2
481	Monitoring and chemistry of aquatic pollutants	K. R. Bull	1
484	Chemical technique development	M. French/D. Roberts	2
485	Chemical support studies	S. E. Allen	2
486	Engineering development	G. H. Owen	9
487	Microprocessor development studies	C. R. Rafarel	9
489	Glasshouse and nursery maintenance	R. F. Ottley	5
490	Photographic development	P. G. Ainsworth	1
491	Radiochemical development	J. A. Parkinson	2
553 +	Radionuclide pathways	K. L. Bocock	2
710 +	Airborne pollutants and Scots pine	J. N. Cape	5
771	Chemical data bank — Monks Wood	K. R. Bull	1

CULTURE CENTRE OF ALGAE AND PROTOZOA

445	Systematics & distribn of smaller algae & protozoa	J. H. Belcher	12
446	Cytology of protists	D. J. Hibberd	12
447	Freshwater and marine amoebae	F. C. Page	12
449	Preservation of cultures	G. J. Morris	12
610	Computerization of CCAP records		12
723	Characterization of Trypanosomes from bats	J. R. Baker	12
724	Study of Trypanosoma of wild British animals	J. R. Baker	12
748	Temperature limits of growth for Chlamydomonas	S. A. Leeson	12

DIRECTORATE

203	The Cinnabar moth	J. P. Dempster	1
393	Isolation effects in butterfly populations	J. P. Dempster	1
408 +	Arboriculture: selection	F. T. Last	5
503	Development of systems analysis	J. N. R. Jeffers	2
504	Markov models	J. N. R. Jeffers	2
508	Botanical variation in elm	J. N. R. Jeffers	2
511	Landscaping at Swindon	F. T. Last	5
517	Primary productivity in woodlands	J. N. R. Jeffers	2
518£	UNESCO MAB information system	J. N. R. Jeffers	2
526 +	Biological monitoring in Forth Valley	F. T. Last	5
629	Systems analysis of Egyptian deserts — REMDENE	J. N. R. Jeffers	2
695	Effects of mycorrhiza on tree growth	F. T. Last	5

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Commissioned Research Contracts

listed by customer organizations for 1981

COMMISSIONED RESEARCH CONTRACTS UNDERTAKEN DURING 1981

Customer	*Project number*	*Project title*
Nature Conservancy Council	138, 181, 461	Toxic chemicals and pollutants
	204	Butterfly monitoring scheme
	208/9/11, 557, 656	Recording of data on individual species
	242	Herb rich swards
	291/2	Population ecology of bats
	466	British Rail land
	549	Pinewood monitoring
	599	Bracken control on heathland
	615	Fragmentation of heaths and invertebrates
	718	Effects of drainage on wildlife
	732	Site management information systems
	–	Rare plant species records
	–	Advice and services
Department of the Environment	380, 452, 583	Sulphur pollution
	408	Arboriculture
	526	Biological monitoring in the Forth Valley
	553	Radionuclides
	567	Vegetation to combat coastal erosion
	573	Amenity grass
	609	River communities (joint FBA)
	625 (pt)	Upland management and water quality (joint FBA/IH)
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