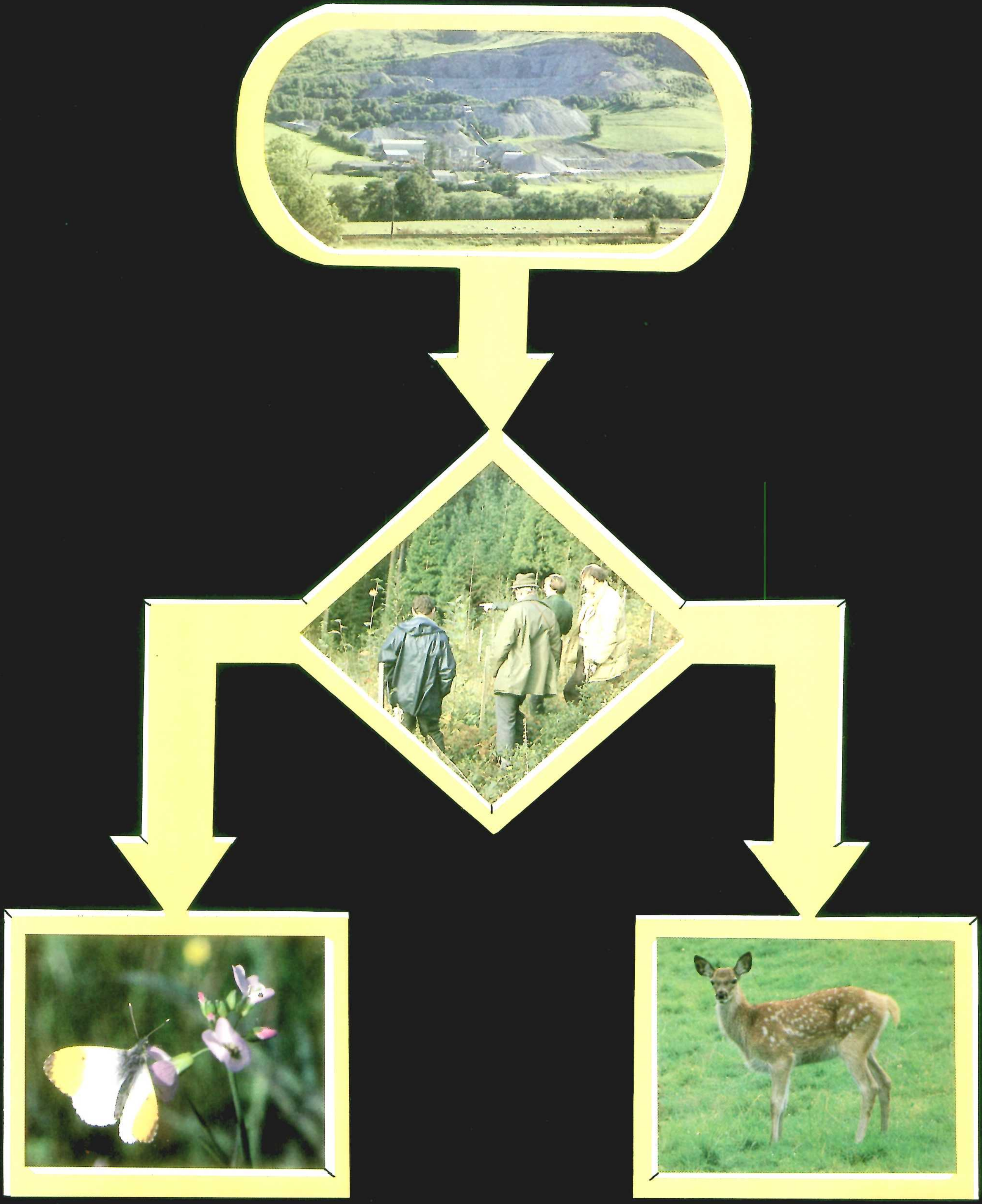
Natural Environment Research Council

Institute of Terrestrial Ecology



1984

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Annual Report 1984

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the rapidly permeating methanol, cellular damage was not observed even at osmolalities of 6000 mOsm. These results suggest, therefore, that osmotic shrinkage and rehydration, rather than increased osmolality *per se,* determine cellular viability.

When suspensions of *S. cerevisiae* were prepared in non-permeating additives (sodium chloride and glycerol), it was found, when using light and electron microscopes, that there was limited plasmolysis (separation of the protoplast from the cell wall) in addition to cell wall shrinkage (Plate 16). Using a specially constructed light microscope stage, enabling volume and surface area changes to be determined accurately, it has been found that cellular shrinkage occurred in hypertonic solutions of sodium salts (Cl^-, I^-, Br^-, NO^{2-} acetate), chlorides (Na^+, CS^+, Li^+, Rb^+, $NH_4{}^+$, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, choline) and non-ionic solutes (proline, glycerol, glucose, glycine-betaine). Thirteen strains of *S. cerevisiae,* and 14 of other species of yeasts responded similarly. In contrast, other cells with walls (eg plant tissue cultures and algae) plasmolyzed when exposed to hypertonic solutions at 20°C. Because this plasmolysis did not happen to *S. cerevisiae,* it seems that plasmalemma and cell walls are closely inter-linked: a possibly important determinant of cellular injury during freezing and thawing.

Using freeze-fracture electron microscopy of shrunken cells, it has been possible to identify major alterations in the organization of plasmalemma and cell walls with the appearance of novel structures which may have been formed by localized plasmolysis or by the projections of cell wall tissue into cytoplasm (Plate 17). These structural alterations were observed following exposure at 20°C or 0°C to solutions of either sodium chloride or glycerol, more concentrated than 2500 mOsm: they did not occur in hypertonic solutions at less than 2000 mOsm. Upon rehydration, these novel changes in cellular ultrastructure disappeared – they are reversible. They were not seen when rapidly permeating compounds (eg methanol) were used, even at concentrations of 5000 mOsm.

It is generally assumed that the primary site of cellular injury, induced by osmotic shrinkage and rehydration, is the cell membrane; the cell wall is not considered significant in determining cellular responses to osmotic and rehydration stresses. However, in *S. cerevisiae,* changes in cell walls were evident following shrinkage and rehydration either at constant temperatures or following freezing and thawing. Enzymic treatments which break down the cell walls of control, untreated, cells are ineffective against cells which have been through a shrinkage and rehydration cycle. The precise biochemical nature of the implied change in cell wall structure is currently being investigated. Is the change a primary cause of freezing or a secondary pathological effect?

Selective effects of freezing

Growth conditions before freezing may modify resistance to freezing injury; it has already been established that cells of *S. cerevisiae* maintained at both sub- and supra-optimal temperatures were more resistant to freezing injury than cells from cultures kept at the optimum temperatures for growth (24°C). Light microscope examination of the resistant cells cultured at 42°C (supra-optimal temperature) showed that they were morphologically distinct from those in cultures maintained at 24°C; they were smaller, and without mitochondria (when stained with specific histochemical stains). This absence was substantiated when the triphenyltetrazolium chloride overlay assay confirmed that more than 95% of cells grown at 42°C were respiratory-deficient mutants; at lower temperatures, there were fewer than 0·1% of these mutants.

As yet, factors conferring resistance to freezing injury on the respiratory-deficient mutants have not been determined. However, our observations demonstrate that, if there is a reduction in viability following cryopreservation, there is likely to be an enrichment of the population with pre-existing, freezing-resistant, respiratory-deficient mutants. While this enrichment might not be important – mutants would be rapidly outgrown by wild types — this system provides a useful model to investigate selection following cryopreservation and other methods of maintenance.

G J Morris, Glynis E Coulson, Lynn C Winters, Karen Jackson and K J Clarke

Programme 8
ECOPHYSIOLOGY AND POLLUTION IN ANIMALS

FACTORS ASSOCIATED WITH THE VARIATION IN THICKNESS OF GREY HERON EGGSHELLS

The thickness of eggshells of the grey heron (*Ardea cinerea*) has been inversely correlated with the concentration of DDT metabolites (mainly DDE) in the egg contents, and measuring shell thickness has been suggested as a rapid and economical bioassay of DDE levels (Cooke *et al.* 1976). Marquiss (1983) collected eggshells in 1981-82 from 32 Scottish heronries, and demonstrated not only variation in the thickness of hatched eggshells between regions and habitats (presumed to be associated with varying DDE levels), but also variation associated with embryonic development and whether or not eggs were successfully incubated. With a sample of 88 heron eggs, with no embryonic development, the relationship between the thickness of an egg's shell and the DDE concentration of its contents is highly variable (Figure 50). Some of this variation is due to the variation in shell thickness within clutches, but this is of little help in assessing samples of shells from many heronries, where nests are high up and close together, so that hatched shells from different clutches mingle when they are cast out of the nest by the parent and become indistinguishable once on the ground. Thus, for most colonies, only large, unbiased samples of shells are useful to quantify relative shell thickness and to imply more or less DDE contamination. Samples of hatched eggshells are not entirely satisfactory, because of bias due to the exclusion of the thinnest of shells which are broken soon after egg lay. To correct this bias, it is important to quantify the variation in thickness due to embryonic development, so as to apply a correction factor to the shells of unhatched and broken eggs, in order to combine them with the samples of hatched shells of similar provenance. Moreover, applying such a correction factor enables an assessment of the bias in shell thickness data from undeveloped but 'addled' eggs, compared with those that have hatched.

Variation associated with embryonic development

As an avian embryo develops, it takes calcium from the inside of the eggshell, which accordingly decreases in thickness. In domestic fowl eggs, shell thickness remains constant until two-thirds of the way through incubation, and then it decreases linearly until the time of hatch, when the shell is about 90% of its initial thickness (Tullet & Burton unpublished). In the heron's shell, thinning is likely to be less, because the hatching chick has less well-developed bones. For a large sample of shells from 1981-82, the mode in the thickness of hatched shells was about 93% of the principal mode for broken (undeveloped) shells (Marquiss 1983, Figure 46). Unfortunately, it was unknown to what extent the sample of broken shells was biased because of the inclusion of shells broken because they were thin. To overcome this problem, a population from an unpolluted site was sampled in the Outer Hebrides, where shells were so thick that there was little chance of any less than 240 μm, below which thickness they would be liable to break because they were too fragile (Cooke *et al.* 1976). Levels of DDE are very low in heron eggs from the Hebrides. No DDE was detected in 11 of 17 clutches examined, and the highest concentration recorded was 1·44 ppm dry weight. The thickness of heron eggshells from the Hebrides was no different from those from elsewhere prior to the advent of DDT in the environment (a sample of 56 Scottish heron eggshells collected before 1947 and now preserved in museums – Figure 50). The mean (± standard error) thickness of hatched shells was 285·5 ± 2·0 μm (n=111), about 94% of the value (303·3 ± 2·9 μm; n = 75) for the shells of undeveloped eggs. The reduction in shell thickness associated with complete embryonic development in heron eggs is thus about 6%, a figure close to the previous estimate of 7% from polluted populations.

By analogy with the pattern of shell change in the domestic fowl, heron shells should commence thin-

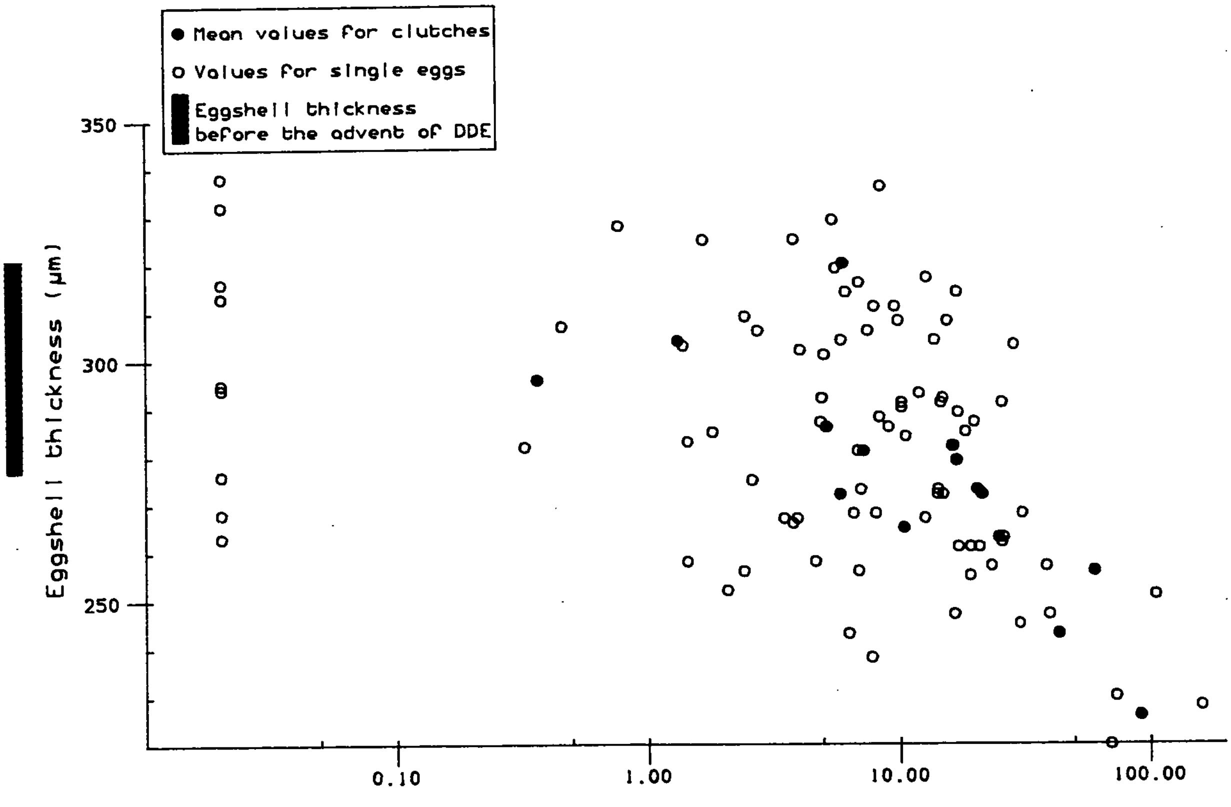

Figure 50 The relationship between the DDE contents of heron eggs and shell thickness for eggs analysed in 1981-83. The range for 56 shells laid before the advent of DDE in the environment is shown to the left of the abscissa

ning between the 15th and 17th day of incubation and do so linearly, reducing to 94% of their initial thickness by hatch on the 25th day. This crude model can be used to estimate the shell thickness of undeveloped eggs from the measured thickness of hatched or partly developed eggs.

Sampling bias of addled eggs

Addled eggs are unhatched and dead eggs where there is little or no embryonic development. They have often been used as samples for chemical analysis to assess pollutant burdens in populations of rarer birds of prey, where to take live eggs would reduce production unacceptably. Their shell thicknesses are often compared with those of eggs in collections made prior to 1947, to assess the extent of shell thinning, and, by implication, the extent of DDE contamination. From the 1981-82 sample of heron eggshells, it was obvious that addled eggs generally had thinner shells than viable eggs, because they were of similar thickness to hatched eggshells, yet could not have lost calcium from the shell because they were undeveloped. Figure 51 compares the average thickness of small samples of shells from addled eggs with the estimated initial shell thickness of viable eggs of similar provenance. Addled eggs were generally thinner-shelled by about 2%, perhaps because thinner-shelled clutches tended to contain addled eggs, or because addled eggs within clutches tended to be those with thinner shells. The latter point was tested by examining 20 clutches where the fortunes of all eggs were known, and where all shells had been retrieved and measured. Addled eggs were thinner than viable eggs within the same clutch (Figure 52), such that the sample of addled eggs from these clutches would have under-estimated overall shell thickness by 2·5%.

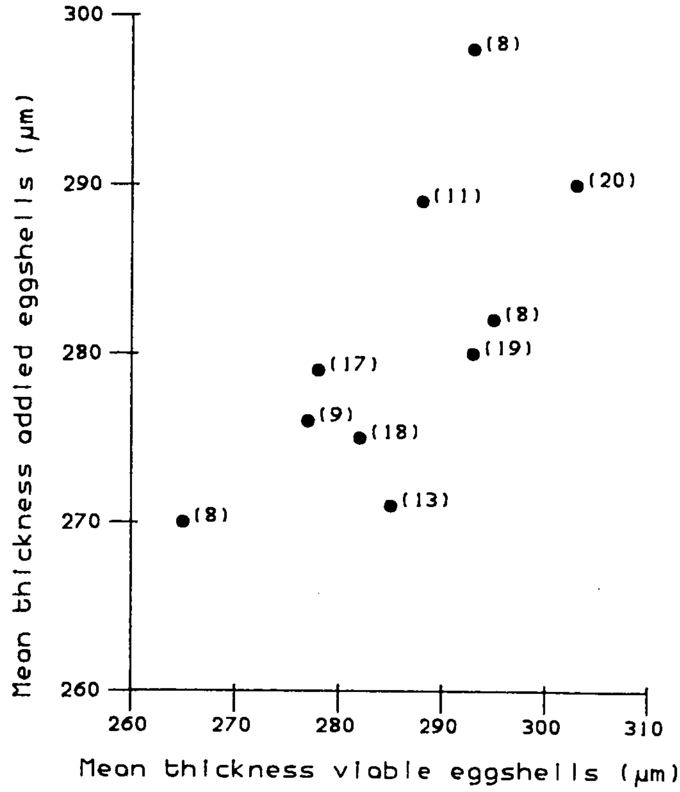

Figure 51 The average thickness of eggshells from samples of addled eggs (sample size in parenthesis), compared with average values for large samples of viable eggs, estimated retrospectively from hatched eggshells from the same colony. Data from 10 colonies in 1981-83

This result raises the question as to whether addled eggs contain more DDE than do viable eggs in the same clutch. This question is not easily resolved, as DDE residue levels in undeveloped eggs may not be strictly comparable with levels measured in well-developed (viable) eggs that have undergone biochemical changes. However, it is possible to examine DDE levels in undeveloped eggs within clutches wherever more than one egg from a clutch has been chemically analysed. For 2 clutches of 5 eggs and one of 4, there was no suggestion of a relationship between DDE content and shell thickness within the whole clutch (Figure 53). In a further 9 clutches, 2 or 3 eggs from the same clutch could be compared for thickness and DDE content. In only 20 instances did the thicker-shelled egg contain less DDE. There was no evidence to suggest that thinner-shelled eggs within a clutch contained more DDE than the rest.

On a broader scale, there was no suggestion that egg addling was directly related to DDE contamination. At some colonies, less than one in 30 clutches contained at least one addled egg, whereas at others the ratio was one in 5. The proportion of clutches containing addled eggs in any single heronry tends to be consistent from one year to the next (data for 8 colonies in 1981 and 1982, $r = 0{\cdot}806$; $P < 0{\cdot}02$). Heronries that had the greatest incidence of egg addling were not those where shells were thinnest ($n = 14$, $r = 0{\cdot}015$; NS), neither were they those where samples of eggs contained the greatest concentration of DDE ($n = 10$, $r = 0{\cdot}390$; NS).

Moreover, there was no evidence that DDE caused embryo deaths directly through the process of shell thinning. Heron eggs that are heavily contaminated with DDE have thin shells, with more pores than those of uncontaminated eggs, so that eggshell porosity tends to increase, but not to the extent that the embryo will suffer dehydration. Any egg with a shell affected enough to suffer excessive water loss is likely to be lost in any case, as it is fragile and breaks soon after egg lay (Burton *et al.* 1985). Here lies the main bias in sampling herons' eggs for assaying DDE content, because the most contaminated clutches have thin shells and soon break. At the worst affected Scottish heronries, such fragility occurs rarely (1 in 16 clutches) and is thought not to be a major problem.

Sampling bias with season

There is yet another potential bias in the collection of eggshells from heronries, pertaining to the timing of

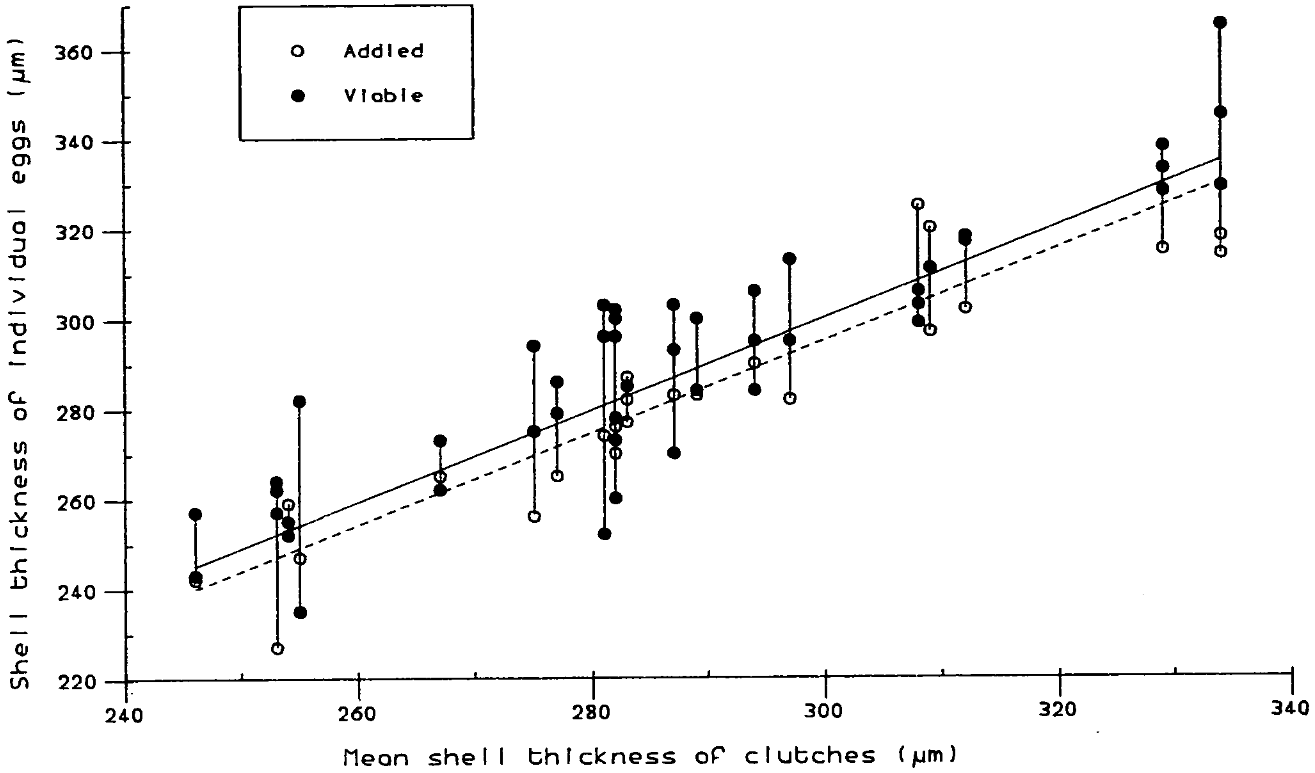

Figure 52 The thickness of addled eggshells compared with those of viable eggs estimated retrospectively from their hatched shells. The solid line (y=x) connects the mean shell thickness of all clutches. The dotted line is the regression line (y=x−6·2) for addled eggs

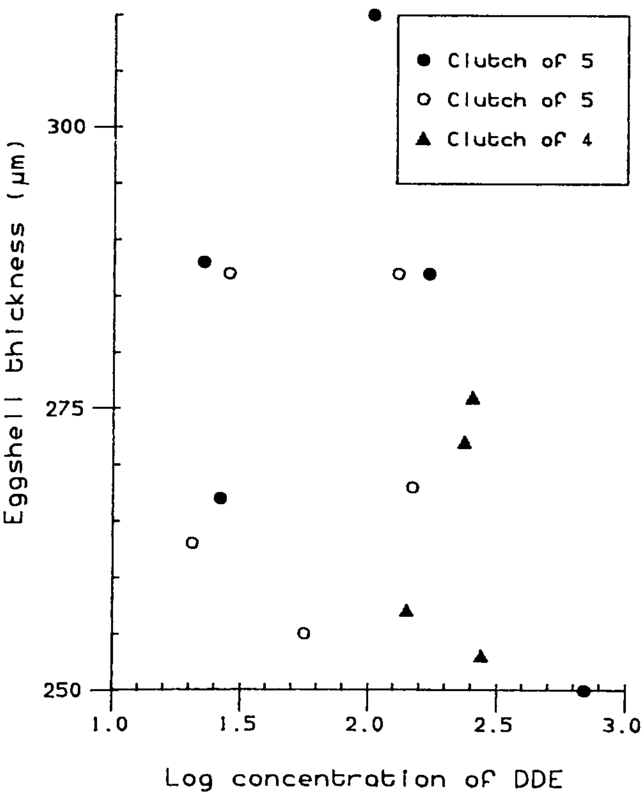

Figure 53 The thickness of eggshells compared with their DDE content for 2 clutches of 5 eggs and one of 4

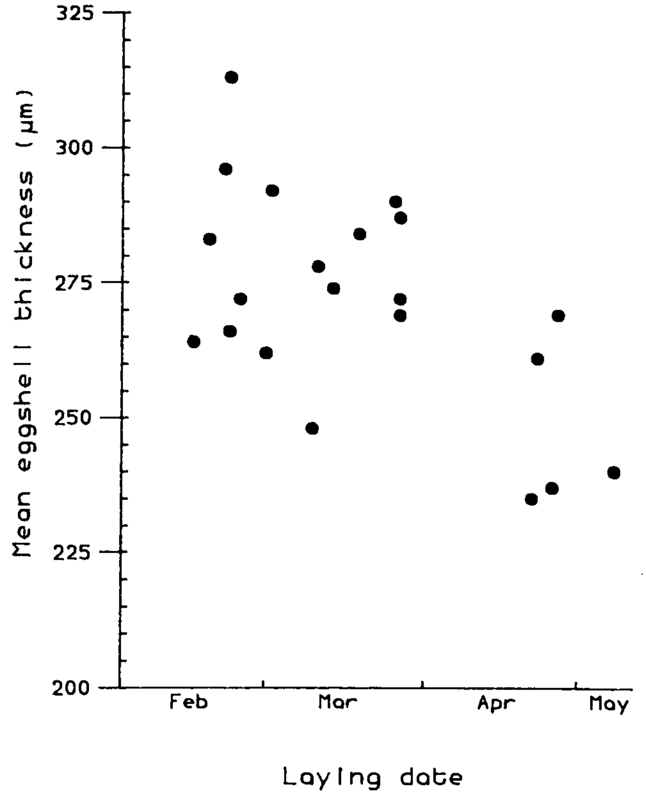

Figure 54 The mean thickness of eggshells per clutch relative to laying date for 21 clutches at one colony in 1981. Circumstantial evidence suggested that the last 5 to be laid were second breeding attempts following failure of the first

collections relative to heron breeding. Eggs laid late in the season have thinner shells than those laid earlier (Figure 54). There is strong circumstantial evidence that these late clutches are a second attempt at breeding, following failure of the first. The number of late clutches is usually equal to the number of earlier failures in the same colony, and a late clutch is often laid in the same nest as, or at least close to, an earlier failure. Late clutches usually hatch well after most nests contain large young, and shell collections can be organized to precede, or at least distinguish, late clutches. Sometimes clutches are lost early in the season and second attempts would then fall within the normal egg laying period for that colony. It is fortunate that this happens infrequently because it is difficult to identify such clutches without several visits to record the fortunes of all nesting attempts.

To summarize, the relationship between eggshell thickness and the DDE content of heron eggs shows considerable variation and any attempt at bioassay using eggshells requires large unbiased samples. Obtaining such samples is possible by using shells collected from colonies, provided that a correction is applied to those shells which had hatched, or contained part-developed embryos. Shells from very late clutches should be avoided. The use of addled eggs exclusively introduces a bias in estimates of shell thinning, as addled eggs under-estimate the population mean by about 2·5%. The use of addled eggs for chemical assay of DDE residues appears to be biased only so far as the most contaminated eggs are fragile and do not survive incubation to be collected intact.

M Marquiss

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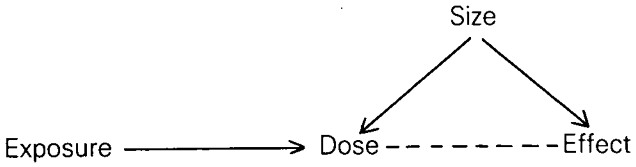
SIZE COUNTS IN ECOTOXICOLOGY

Contaminants in the abiotic environment become pollutants when they affect living organisms: exposure results in organisms acquiring a dose of pollutant, and the probability or severity of an effect increases with the dose. Size of animal can affect both dose and effect, in ways than can be both important and not generally appreciated:



The concept of dose can become quite sophisticated. Indeed, we do not yet really know how to measure dose in wildlife (Moriarty 1983). In practice, the amount of pollutant present at one time within an animal is usually taken as the measure of dose and, to allow for the effect of body size, this amount is expressed in units of concentration – so much weight of pollutant per unit weight of animal. Data of this type are then commonly used for 2 purposes:

1. to compare the degree of environmental contamination at different sites or times;
2. to indicate the degree or likelihood of biological effect to be expected on individual organisms.

Two examples are given to indicate the differences of interpretation that can arise from use of concentrations when no further account is taken of any differences in animal size.

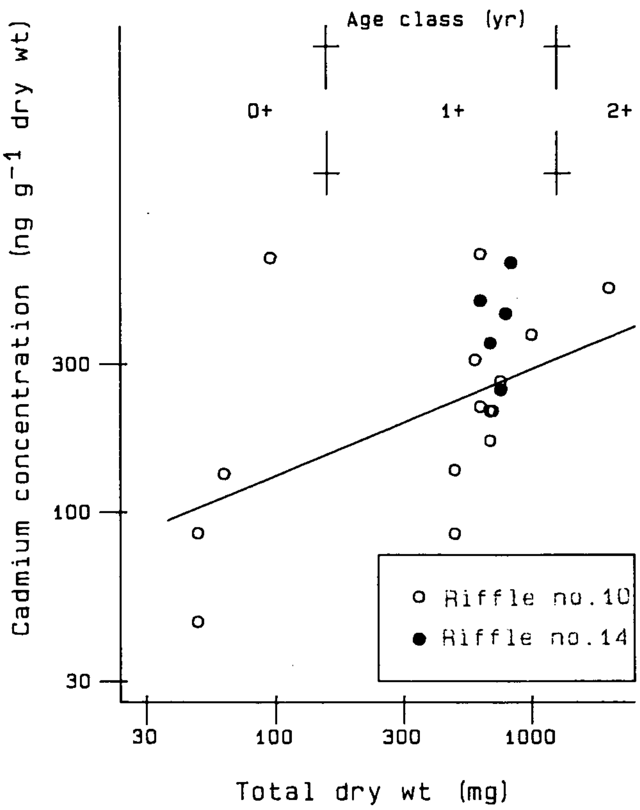


Figure 55 Cadmium concentrations and dry weight of female bullheads taken, on 5 August 1981, from riffles 10 and 14 in the River Ecclesbourne, Derbyshire. A linear regression of the form y=a+bx has been fitted to the data for riffle 10, where y and x are the logarithmic values of the metal concentration and dry weight, respectively. Data from Moriarty et al. *1984*

Assessing the degree of environmental contamination
The sediments of the River Ecclesbourne, Derbyshire, are contaminated with cadmium, and it was of interest to see whether fish taken from different riffles contained different amounts of cadmium. The linear regression in Figure 55 shows clearly that heavier fish contain higher concentrations of cadmium. In situations of this type, comparisons of mean concentrations in different samples are usually restricted to individuals that fall within similar and restricted ranges of weight. Fish of the age class 1+ years from riffles 10 and 14 appear to be suitable for comparison: fish from riffle 14 were, on average, 11·4% heavier than fish from riffle 10, a difference that is statistically insignificant (t_{13} = 1·091, P>0·020). Cadmium concentrations in these 2 samples, when compared in the conventional manner by a t-test, did appear to differ (t_{13} = 2·139, P ~ 0·054). However, analysis of covariance, which removes the effect of individual differences in body weight from the comparison, gave less convincing evidence for a difference of cadmium concentration ($F_{1,12}$ = 2·92, P ~ 0·115).

Considerations of this type cast doubts on the validity of some monitoring programmes, where it can be demonstrated that inadequate account is taken of differences in body weight, and there is a risk of false conclusions (eg Figure 56). The OECD co-operative study on chemical trends in wildlife concluded from

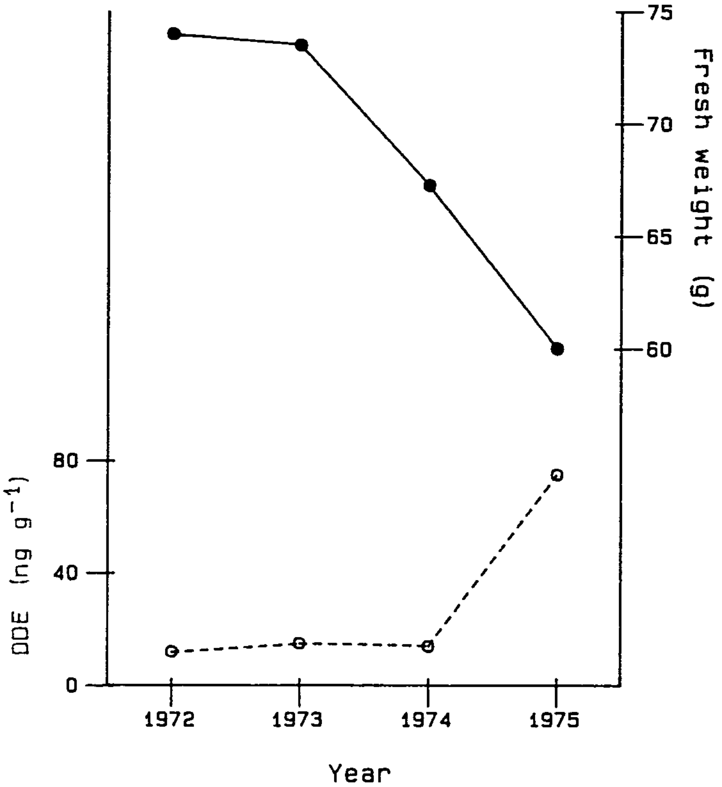


Figure 56 Concentration of p,p'–DDE *in pectoral muscle and fresh total body weight, in samples of 10 14-day-old nestling starlings taken in 4 consecutive years at Kvismaren, Sweden. Data from OECD 1980*

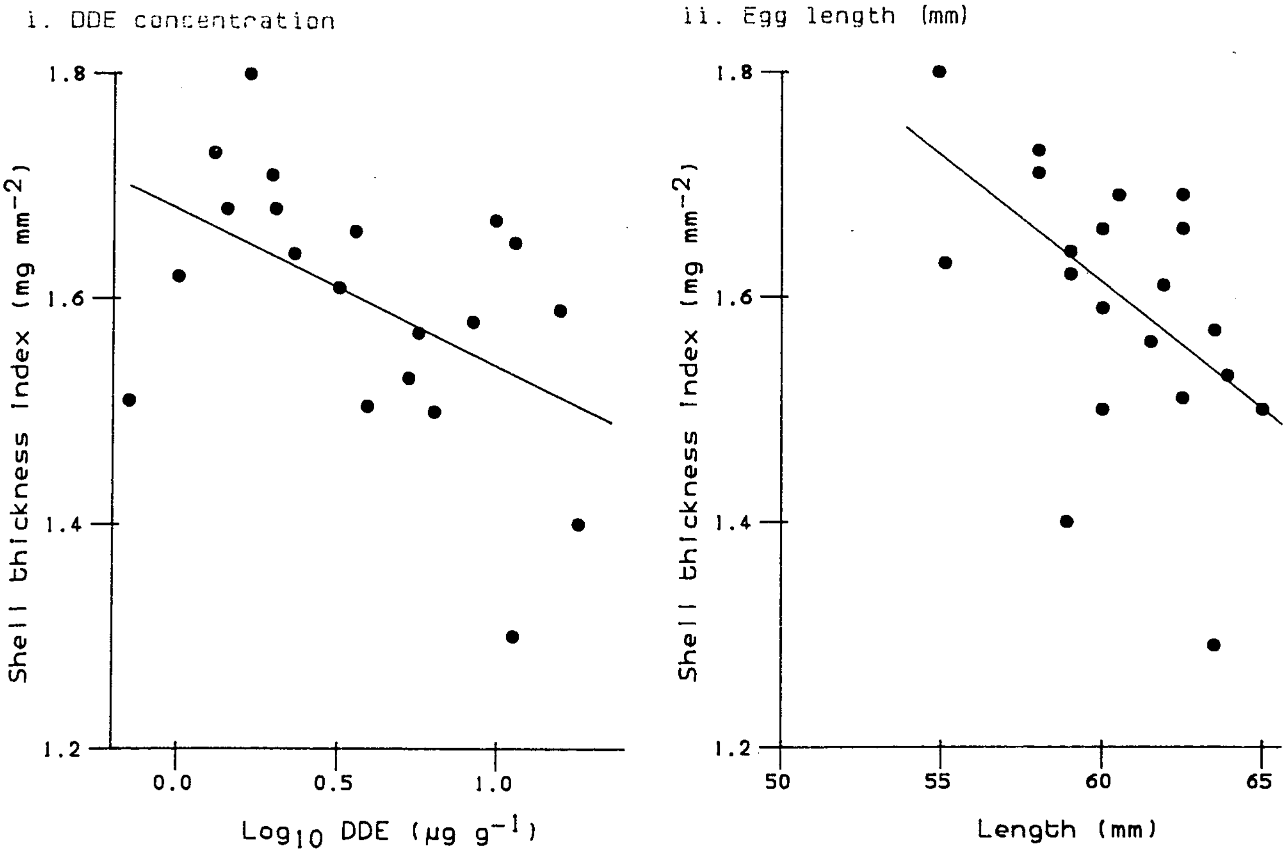


Figure 57 Linear regressions of Ratcliffe's index of shell thickness on the p,p'–DDE *content of eggs and on maximum egg length in a sample of heron eggs taken from Troy, Lincolnshire, in 1968. Data from Moriarty* et al. *in prep*

these data, plus additional measurements on other variables, and after multiple regression of the *p,p'*-DDE concentration on these variables, that there had been a significant increase during the period 1972-75 in the degree of environmental contamination by *p,p'*-DDE. An alternative statement, at least as valid, is that year affects both *p,p'*-DDE concentration and weight of nestlings, and that any inference about the degree of environmental contamination must be speculative. It is interesting to note that the concentration of *p,p'*-DDE increased 4·8-fold in 1975, a significant rise ($d_9=3{\cdot}716$, $P < 0{\cdot}01$), whereas body weight was only 10·7% lower in 1975 than in 1974, a decrease of little statistical significance ($d_{14} = 1{\cdot}385$, $P \sim 0{\cdot}20$), but possibly of considerable biological significance.

Assessing the biological effect

It has been shown for many bird species, from both field observation and laboratory experiment, that eggshells become thinner as their content of *p,p'*-DDE increases, and it is generally supposed that *p,p'*-DDE thins eggshells. However, there is no good reason to suppose that, in the absence of *p,p'*-DDE, eggs of different sizes and shapes will have shells of the same thickness. Figure 57 indicates the difficulties of interpretation that can arise when size is ignored; does *p,p'*-DDE affect shell thickness, egg size, or both? Work on this question is continuing.

F Moriarty, Hazel M Hanson, A A Bell and P Freestone

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LEAD POISONING IN MUTE SWANS

A major objective of this study, which began in October 1981, was to determine the proportion of swan deaths which were attributable to ingestion of lost, or discarded, fishing weights. Bodies were recovered from all parts of Great Britain, but intensive study was confined to fen land incorporating the Rivers Welland, Nene and Ouse, with a total river length in excess of 500 km. On receipt of each carcase, an X-ray was taken and any foreign bodies seen by this means were removed at post-mortem for examination. Lead fragments in the alimentary tract, in particular the gizzard, were shown in most cases to be lead fishing weights. At post-mortem, liver, kidney and bone were removed, and total lead levels in these tissues were then determined by atomic absorption spectrophotometry. Chemical analysis, linked with X-ray and post-mortem findings, revealed that 78% (468) of the 600 swans examined had died of lead poisoning. The pathological effects of such poisoning were the same as described previously (Simpson *et al.* 1979).

Lead weights are eaten by swans (Plate 27) in their attempt to obtain grit, which is used to help break up food in the gizzard. In some urban areas, bread and grain form a substantial part of the daily food of swans, whereas, in other areas, the diet is comprised entirely of green vegetation. Experiments have shown that diet can have a significant effect on lead uptake, probably because of an increased uptake of grit by birds feeding on green food, compared with birds on a total corn diet. In a trial with ducks, individuals fed on green food ingested 3 times more grit than other individuals fed solely on corn. The birds on green food also had higher levels of lead in the livers and kidneys. The grinding activity of the gizzard in this particular group was increased, thus making the lead more available for absorption. An increased grit uptake would also increase the chances of swans obtaining lead fishing weights.

The toxicity of 2 alternative forms of fishing weight has been tested on ducks, one based on tungsten, the other on stainless steel. Both proved to be acceptable toxicologically, and are now available commercially. Finally, we could find no influence of the closed fishing season on the availability of lead to swans. We received as many lead-poisoned birds during the closed season compared with the previous, or following, period of time, and the same proportion had died from lead poisoning. If the alternative weights were used instead of lead, the problem of lead poisoning in many areas would probably take several years to disappear.

M C French

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WILDLIFE INCIDENTS: A SUMMARY FOR 1979-84

(This work is partly supported by Nature Conservancy Council funds)

ITE has a number of investigations in progress on the ecotoxicology of chemicals in the marine, freshwater, estuarine and terrestrial environments. These investigations are mainly of chemicals which are thought to be influencing the breeding, survival and environmental resources (eg food or habitat) of terrestrial wildlife.

Plate 18 Mount Usborne, with glacial cirque and stone runs; at 705 m the Falkland Islands' highest mountain
(Photograph J Miles)

Plate 19 Flowering diddle-dee: this plant predominates on the well-drained soils, covering about 20% of the land
(Photograph J Miles)

Plate 20 Gentoo penguins by Bertha's Beach
(Photograph J Miles)

Plate 21 Eroding inland diddle-dee heath: an example of soil erosion by wind which is widespread in the Falkland Islands
(Photograph J Miles)

Plate 22 A bogged-down tractor testifies to the hazards of driving over the camp, where peaty topsoils and blanket bog predominate, and shows how easily the vegetation can be damaged by vehicles
(Photograph J Miles)

Plate 23 A pair of Falkland Islands' estimated 500 000 upland geese. Geese on the wing are a bird-strike hazard to aircraft at the new airfield
(Photograph J Miles)

Plate 24 Loch Fleet, Galloway, formerly a useful trout loch, but now completely fishless
(Photograph P S Maitland)

Plate 25 A population of marsh orchids that developed naturally on shelly sand dumped at Sizewell 14 years previously
(Photograph D S Ranwell)

Plate 26 Mycorrhizal fungi, like this *Inocybe* species, are not usually thought to be associated with litter decomposition. Studies of their enzyme potential however, suggest that they may be active decomposers
(Photograph J Dighton)

Table 18. Recent wildlife mortality/incident investigations

Species	Scientific names	Area	Date	Incident	Number of animals involved	Cause
1979-80						
Waders, gulls and ducks	*Calidris alpina* *Larus ridibundus* *Larus* spp. *Anas* spp.	Mersey Estuary	Autumn - winter 1979	Dead and sick birds on shore of estuary	>2500	Lead, mainly alkyl lead from industrial effluent
1980-81						
Gulls, waders and ducks	*Larus ridibundus* *Calidris alpina* *Anas* spp., etc	Mersey Estuary	Late summer - autumn 1980	Dead and sick birds on shore of estuary	>800	Alkyl lead (botulism in a few birds)
1981-82						
Various waders, gulls and duck	*Calidris alpina* *Tringa totanus* *Larus* spp. *Anas* spp., etc	Mersey	Autumn 1981	Birds dead and sick on shore	50	Alkyl lead for some
Whooper swans	*Cygnus cygnus*	Glasgow area	Various times in several years	Dead swans on marsh	10+	Lead (gunshot)
Black-headed gulls	*Larus ridibundus*	Ravenglass colony	Various times in several years	Dead birds and reduced breeding success	Colony of many thousands of birds	Unknown (related to Mersey incidents?)
Mute swans	*Cygnus olor*	Essex coast	Various times during winter	Birds behaving abnormally	*c*100	Brewery effluent?
Auks	*Alca torda* *Uria aalge*	Shetlands	Feb-March 1982	Dead birds on shore	600	Food shortage?
1982-83						
Various herons, waders, etc	*Ardea cinerea*, etc	Mersey estuary	Autumn 1982	Birds sick and dead on estuary	*c*100 (14 heron)	Alkyl lead (for herons)
Passerines	Various	Cambridgeshire	Autumn 1982	Birds dead and sick in fields	*c*500	Aldicarb suspected
Geese†	Not informed	East Anglia	Autumn 1982	Birds dead in field	*c*10	Carbophenothion
Gulls	*Larus argentatus*	Near Aberystwyth	January 1983	Sick and dead birds washed ashore	*c*20	Unknown Organs examined appeared healthy
Auks and other seabirds	eg *Alca torda* *Uria aalge*	East coast of UK	Feb-March 1983	Groups of birds dead on shore along east coast of UK	*c*30 000	Food shortage
1983-84						
Gulls*‡ (herring, black-headed, lesser black-backed	*Larus argentatus* *Larus ridibundus* *Larus fuscus*	Thames Estuary	Dec 1983 - Feb 1984	Groups of gulls dead on shore	100+	Unknown
Brent geese*	*Branta bernicla*	Thames Estuary	Autumn 1983 and earlier years	Number of dead individuals on shore	*c*20	Lead
Gulls (mainly black-headed)	*Larus ridibundus*	Peterborough	Oct-Nov 1983	Groups of gulls dead at roost	100+	Various
Sea eagle†	*Haliaetus albicilla*	Norfolk	*c*11 May 1983	Bird sick; died in care	1	Shot
Starlings	*Sturnus vulgaris*	Durleigh Reservoir	31 Jan 1984	Birds dead on water	*c*200	Collision suspected
Starlings‡	*Sturnus vulgaris*	Basildon	Autumn 1983 and earlier	Flightless starlings	*c*50?	Lead?
Gannets	*Sula bassana*	Stranraer	During winter 1984 and previous years	Dead bird, sick birds on shore	?	Starvation?
Heron (and others)	*Ardea cinerea*	Aberystwyth	July 1984	Sick bird died in care	Few	Dived into oil lagoon Probably died of shock

* MAFF investigations to date. Now passed to ITE, except for botulism tests

† Investigation passed to, or mainly dealt with by, MAFF

‡ Incident also involves Essex University Environmental Unit

These incidents have been reported by NCC staff, RSPB representatives, MAFF VIC staff, RSPCA Inspectors, members of the public, and officials of other bodies

The years given in the Table run from approximately March to March, in line with the preparation of a contract report to NCC, who helps finance this work

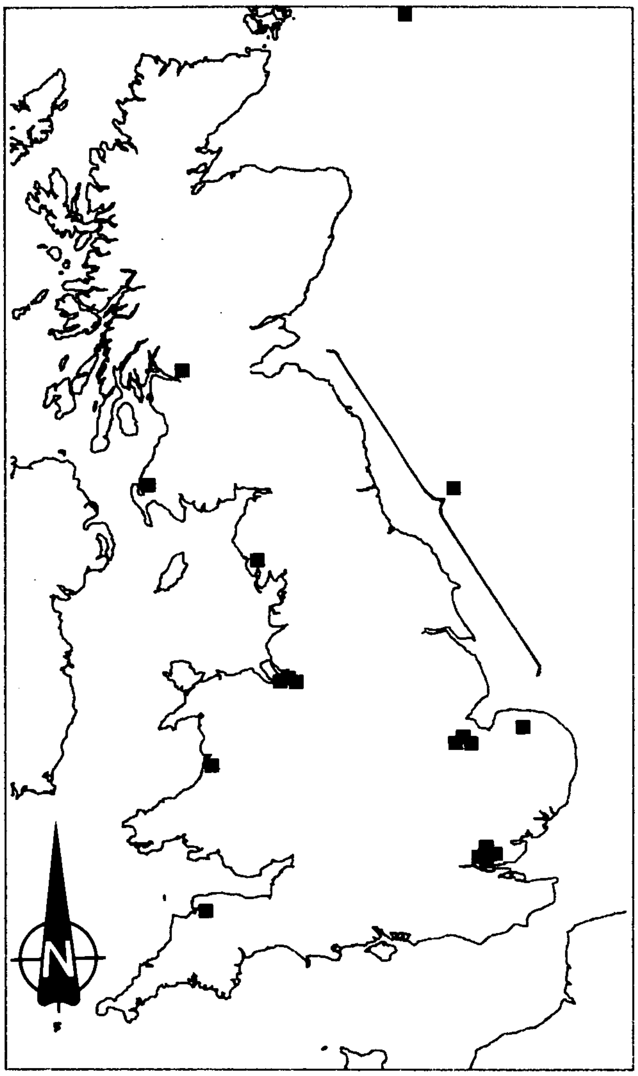

Figure 58 Geographical distribution of incidents investigated

The usefulness of incidents involving wildlife mortalities in providing foci or attention for ecotoxicological studies has led to the Institute maintaining a watching brief on such incidents in Britain, and to the investigation of their causes, alerting experts in other laboratories when necessary.

In recent years, the Institute's laboratories at Monks Wood have been involved in investigating a number of wildlife incidents, most of which have involved birds. Table 18 lists these incidents and indicates the most probable cause of the mortality, and Figure 58 shows their geographical distribution. Table 18 shows that toxic chemicals are only one of the many factors that cause wildlife incidents. Many other factors, such as disease, starvation and accidents, also contribute to loss of wildlife.

Those incidents which involve small numbers of animals are not usually investigated in any great detail, and the Institute's advice is sometimes all that is needed for a problem to be resolved. However, in certain cases, even incidents involving small numbers of animals need to be investigated thoroughly, perhaps because the small numbers of deaths reported indicate a much larger mortality. For example, if birds are found on isolated marshes visited by few people, it could be that a more thorough search would reveal more corpses.

Typically, members of the public, regional officers of voluntary bodies (eg RSPB, RSPCA, BTO), or Government departments (eg NCC or MAFF) inform ITE of an incident and animals are sent to the laboratories at Monks Wood, where post-mortem studies and X-rays are carried out. These investigations reveal whether the animals involved have met with an accident, or have any unusual features to indicate that they died from disease, or have been poisoned by certain chemicals which have specific effects on particular organs.

The next step is to analyse tissues, usually the liver and one other tissue (eg brain, muscle, or kidney), for chemicals which are known to have caused mortality incidents in the past. On the basis of this work, it is usually possible to suggest the likely causes of death. However, there are inevitably times when the cause of death cannot be ascertained.

Once the cause of an incident has been determined, deciding on its importance, and on the need for more detailed investigation, is often difficult. There are many reasons for this difficulty. First, the deaths of a few animals may not seriously affect the size of the population in any way. Second, the mortalities may be unimportant nationally, but of considerable importance to people living in the area where a pollution problem is discovered. Third, what appears as an isolated incident may, in fact, be one of a series that have not been discovered or reported. Fourth, an event involving a small proportion of an animal population may have a long-term effect on the species, if it is repeated over a period of time and/or affects a particular section of the population (eg if females are more susceptible than males). In short, a considerable degree of uncertainty often remains, even when the investigation of an incident has been completed.

One feature of our work on wildlife incidents is the increase in the number that have occurred in recent years, during a period when pollution controls have become increasingly stringent. Possibly the increase in reports simply reflects the greater awareness of the public to environmental problems and a desire to see them controlled.

Fuller details of the incidents investigated, along with the analytical results obtained, can be found in a series of publications which are listed below.

D Osborn

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HORMONAL CHANGES DURING BREEDING IN FREE-LIVING STARLINGS

Successful reproduction in birds in seasonal environments requires an accurately timed succession of changes in reproductive state and behaviour. Such temporal organization necessitates mechanisms to predict favourable conditions many weeks in advance, as well as to co-ordinate changes during the breeding cycle. The integration of these changes is largely brought about by a changing balance of various pituitary and gonadal hormones, whose secretion is influenced by environmental and behavioural cues.

Three pituitary hormones are important in reproduction. Two of them, luteinizing hormone (LH) and follicle-stimulating hormone (FSH), are gonadotrophic; they stimulate growth and maturation of the gonads, and LH, in particular, also stimulates the gonads to secrete steroid hormones. The third hormone, prolactin, is involved with incubation and other 'parental' behaviour and induces development of the brood patch. In pigeons, it also causes production of 'crop milk', on which the young are fed. This characteristic is analogous to its role in mammals where it stimulates milk production.

It has been known for many years that long daylengths cause increased secretion of LH and FSH. Studies at ITE, in collaboration with Bristol University, have recently shown that, in starlings (*Sturnus vulgaris*) at least, this effect is also caused by prolactin, but that prolactin secretion requires a longer daylength than the 2 gonadotrophins (Ebling *et al.* 1982; Dawson & Goldsmith 1983). Thus, during gradually increasing daylength in spring, there is an increase in gonadotrophin secretion followed by an increase in prolactin secretion. We have found that the broad temporal patterns of change in blood concentrations of gonadotrophins and prolactin during the year are similar in captive non-breeding birds (Dawson & Goldsmith 1982, 1984). However, absolute levels, particularly of prolactin, and fine temporal adjustments are somewhat different. Breeding behaviour is therefore important in modifying the underlying photoperiodically driven changes.

A series of experiments, 2 of which are described here, was carried out on starlings to determine the

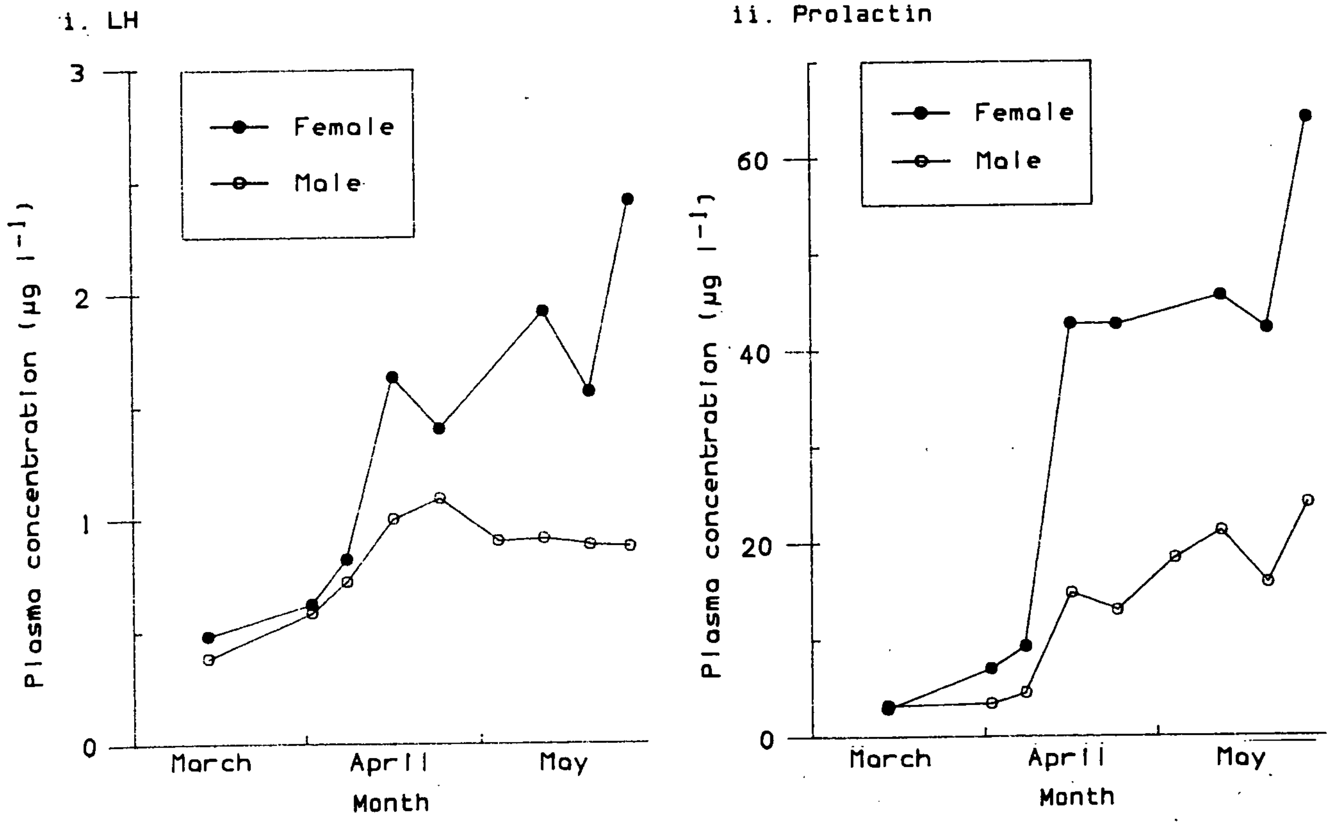
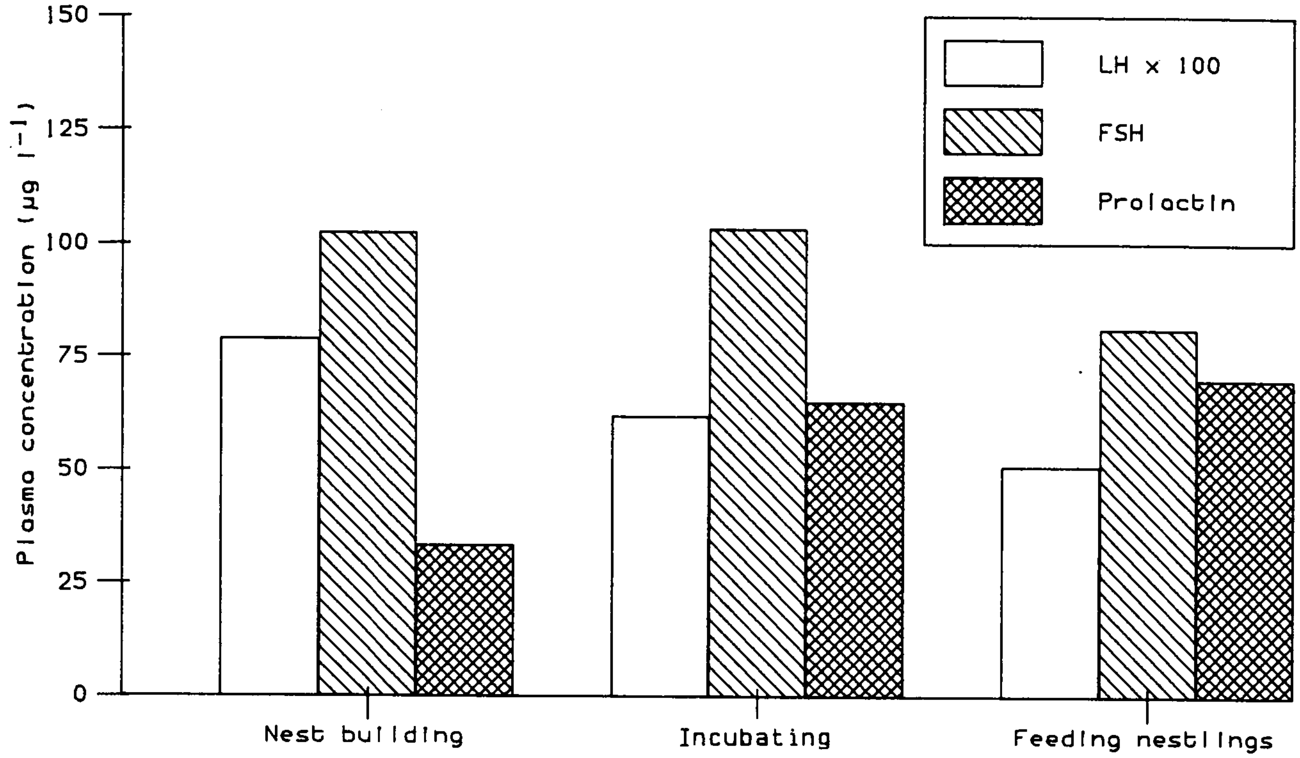


Figure 59 Plasma concentrations of (i) LH and (ii) prolactin in male and female starlings sampled whilst nest building between early March and late May

i. Males



ii. Females

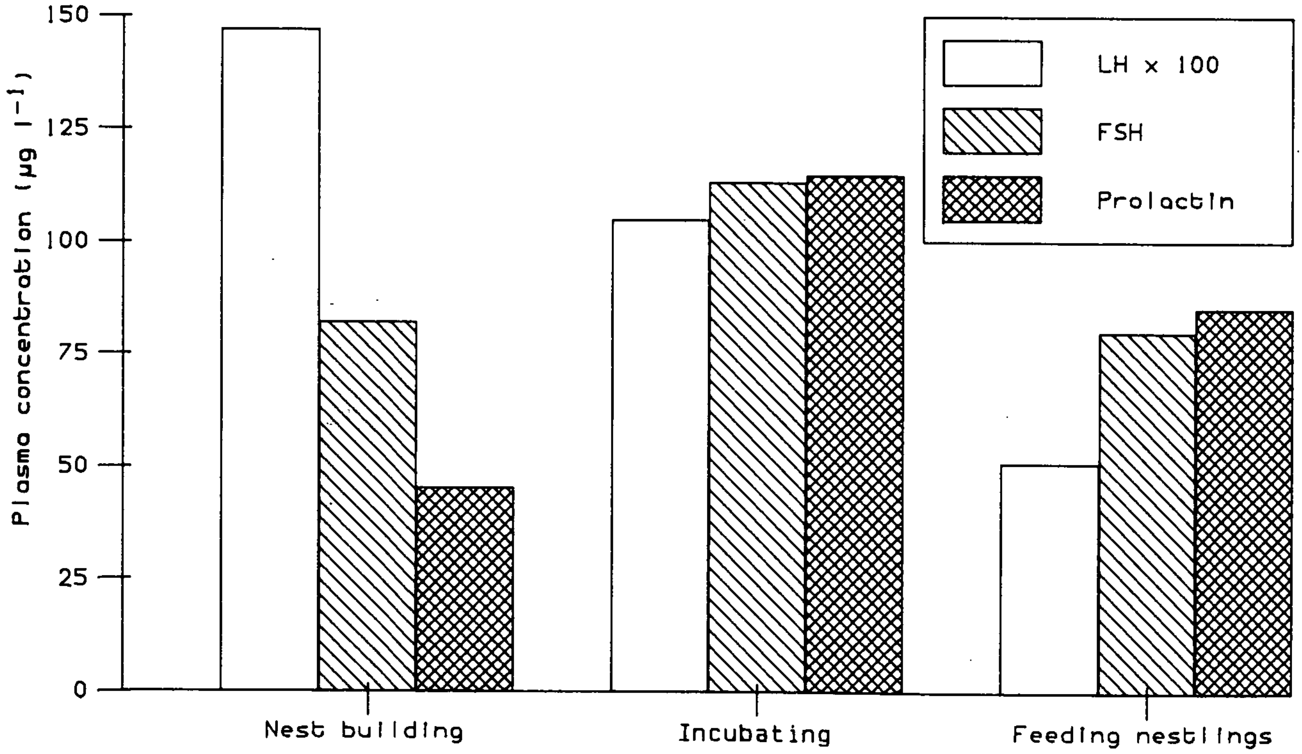


Figure 60 Plasma concentrations of LH, FSH and prolactin in (i) male and (ii) female starlings sampled between 9 May and 12 May but during different stages of breeding

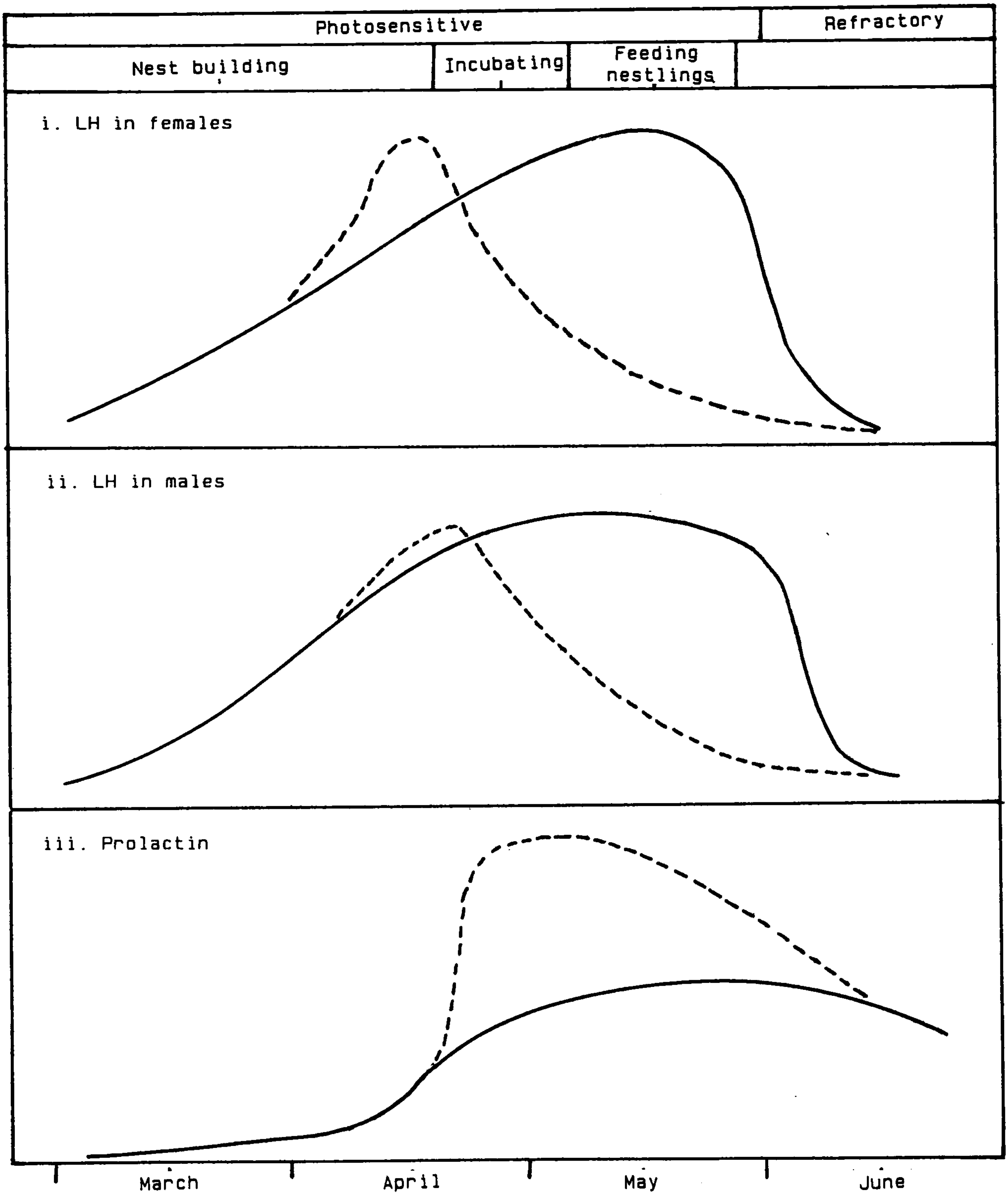


Figure 61 *The relative importance of daylength and breeding behaviour during the breeding season in modulating plasma levels of LH in female and male free-living starlings and of prolactin in both sexes. Solid lines represent changes which would occur in non-breeding birds (ie changes entirely induced by changing daylength), based on results from captive birds held in outdoor aviaries and free-living birds not permitted to progress beyond nest building. The broken lines indicate how these levels are changed by factors directly associated with the different stages of a breeding cycle, nest building, incubation and feeding nestlings, in single brooded starlings*

relative importance of daylength and 'local' factors related to breeding in determining blood levels of reproductive hormones during different stages of the breeding cycle.

Seventy nest boxes have been erected around Monks Wood and at local farms, and starlings nest readily in them. Both experiments involved trapping birds in these nest boxes throughout the breeding season, and taking a blood sample from each bird. Concentrations of the 3 hormones in blood plasma were then measured by radioimmunoassay.

In the first experiment, starlings were trapped and sampled as they were nest building. After release, the nest was removed from the box. This sequence was repeated throughout the breeding season, so that birds were not allowed to lay a clutch or to incubate. These birds were therefore exposed to natural changes in daylength, but not involved in any breeding activity beyond nest building. Plasma LH was already elevated by early March (Figure 59i). In males it increased slightly further throughout April and remained high during May, and in females it increased throughout April and May. Plasma prolactin was low during March and early April in both sexes, but increased during mid-April and remained high during May (Figure 59ii).

In the second experiment, many of the nest boxes in which eggs were laid early in the season were left undisturbed. Other nests were repeatedly removed in such a way that, by the time the undisturbed birds were feeding young, others would be either in mid-incubation or still nest building. Between 9 May and 12 May, as many birds as possible were trapped and sampled, at each stage of breeding. These birds had therefore experienced the same changes in daylength, but were at different states of breeding. Plasma LH was highest in nest building birds, and decreased during incubation and feeding young (Figure 60). Plasma FSH did not change significantly, and plasma prolactin was much higher in birds incubating and feeding young than in nest builders.

By comparing hormone levels in these 2 experiments and in captive birds, we can produce the model in Figure 61. It shows the hypothetical profiles of plasma levels of LH and prolactin which would be driven by changes in daylength in the absence of breeding, and the way in which these are modified by 'local' factors concerned with behaviour during the breeding cycle. Plasma levels of LH increase before breeding in response to increasing daylength. In females, during nest building, LH levels are further stimulated by local factors, such as courtship behaviour. Prolactin secretion is also stimulated by increasing daylength, but, because it requires a longer photoperiod than LH secretion, plasma levels do not begin to increase until later in the year. The presence of eggs in the nest greatly stimulates prolactin secretion over and above that caused by increased daylength. At the same time, LH levels are depressed, possibly by antigonadotrophic effects of prolactin. Finally, in early June, LH levels decline, even in non-breeding birds, as they become photorefractory, ie no longer stimulated by long daylengths, and the levels remain low for the rest of the year.

A S Dawson

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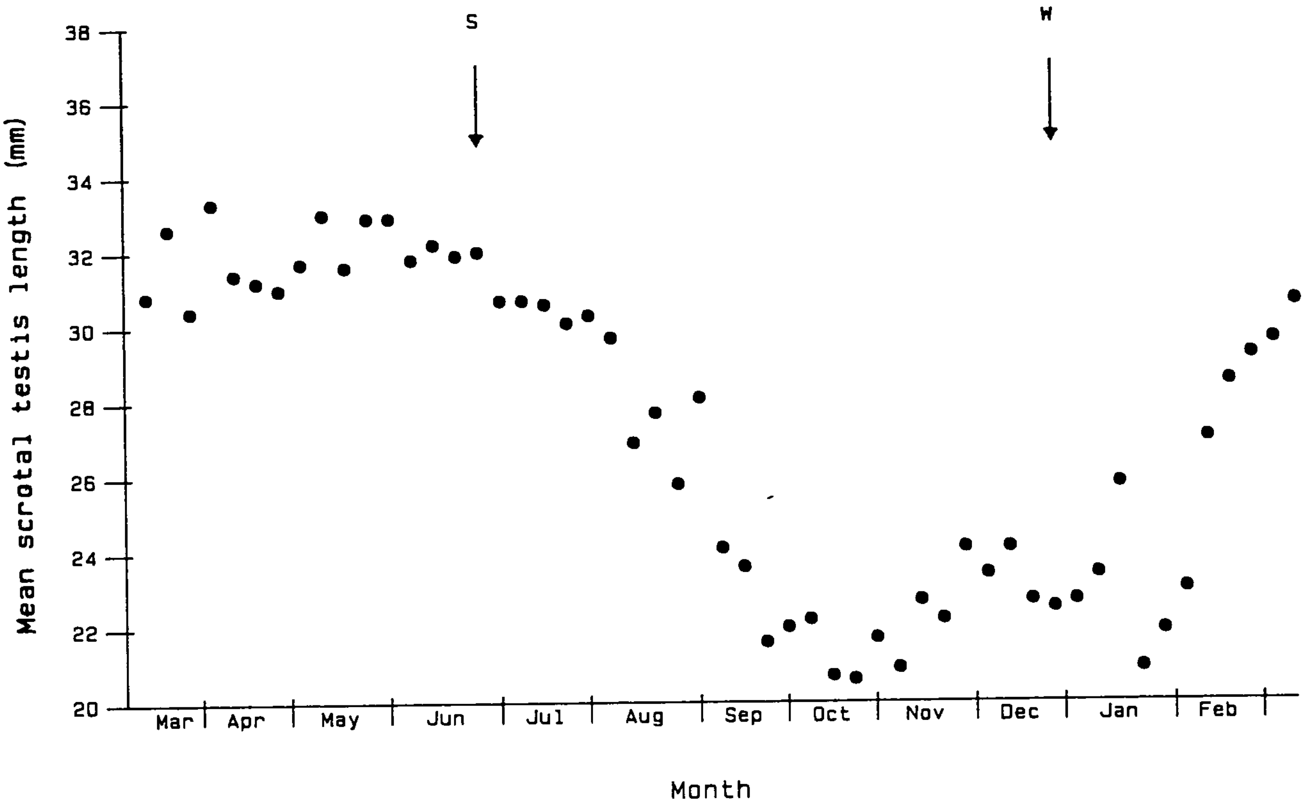
PHOTOPERIODIC REGULATION OF TESTIS DEVELOPMENT IN WILD RABBITS

The testes of wild European rabbits (*Oryctolagus cuniculus*) in northern Europe develop and regress seasonally (Brambell 1944; Henderson 1979; Andersson *et al.* 1979; Davies & Myhill 1980). Seven male wild rabbits (Plate 31), kept in an outdoor enclosure at Monks Wood, showed a similar cycle of testis size over one year (Figure 62) (analysis of variance on repeated measurements, $F_{52,312} = 20{\cdot}741$, $P<0{\cdot}01$). Moult occurred when testis length reached a minimum, and the occurrence of pregnancy in accompanying females coincided with the period when testis length was maximal. *In situ* measurements of testis length are a good indication of the occurrence of spermatogenesis.

The purpose of this study was to determine what role daylength has in regulating the annual cycle of reproductive activity, and, hence, the length of the breeding season. One group (A) of male rabbits, which had been taken from the wild, was exposed to short days (8L:16D) for 8 weeks. Another group (B) was exposed to long days (16L:8D) for 8 weeks. Group A was then transferred to long days, while group B was transferred to short days. Testis length measurements were begun 3 weeks before each transfer. Transfer-

i. Changes in testis length



ii. Frequency distributions

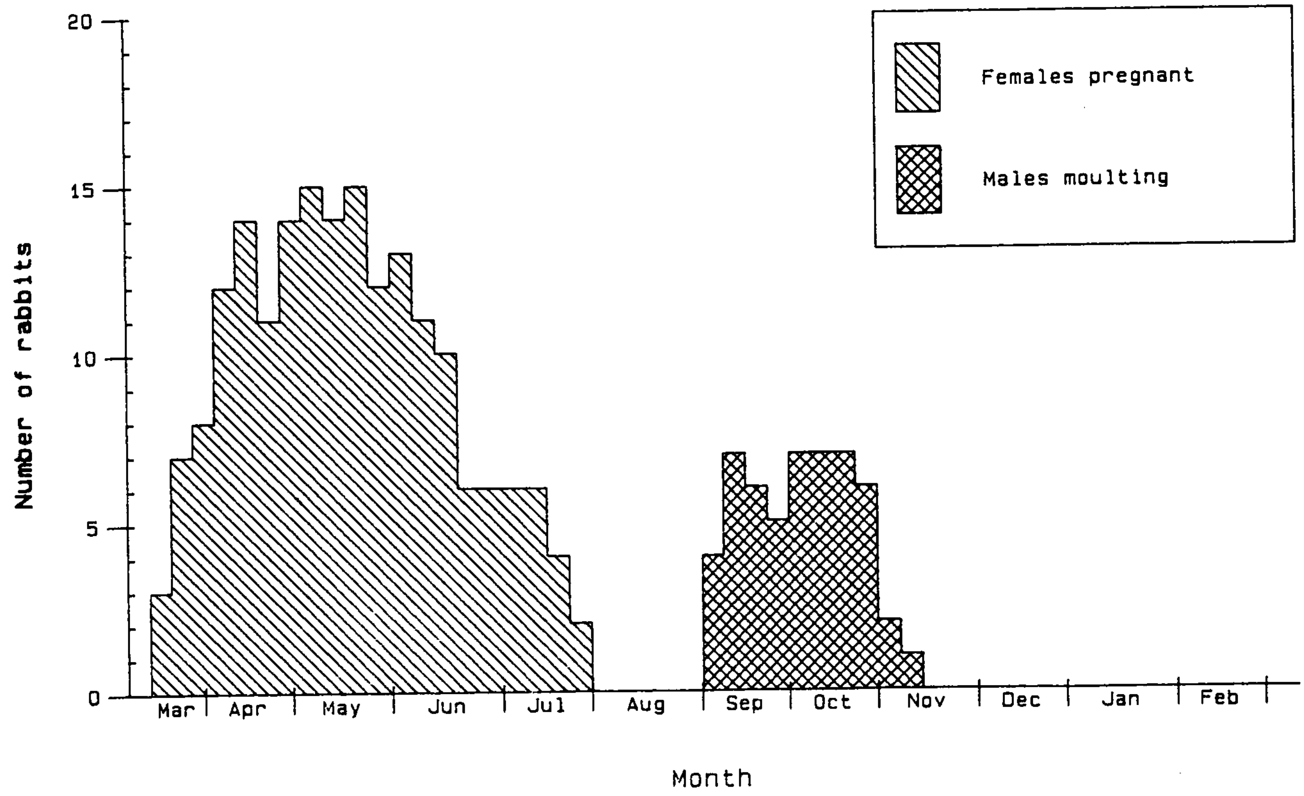


Figure 62

i. Changes in the mean testis length of 7 adult male wild rabbits kept in an enclosure for one year. The time of the summer (S) and winter (W) solstices are marked.

ii. The frequency distributions of moult in these males and of pregnancy in 18 accompanying females with respect to time ring rabbits with regressed testes from short to long days led to an immediate increase in testis length (weeks 1 to 13, group A, $F_{12,36} = 17{\cdot}088$, $P < 0{\cdot}01$), which reached an asymptote 7 weeks after the transfer (Figure 63). Twenty-five weeks after the transfer, no significant decline in testis size had occurred (group A, weeks 14 to 27, $F_{12,36} < 1{\cdot}319$, $P < 0{\cdot}05$) (Figure 63). Rabbits transferred at the same time from long to short days showed a significant decline in testis length (group B, weeks 1 to 8, $F_{7,28} = 13{\cdot}164$, $P < 0{\cdot}01$), but after 8 weeks in short days testis length began to increase (Figure 63). The testes of rabbits in group B had completely regrown 15 weeks after the initial transfer. These rabbits also moulted at the same time as the onset of testis regrowth.

This study has shown that daylength can influence the fertility of wild rabbits. Prolonged exposure to long days does not lead to testis regression. Transferring rabbits from long to short days, which simulates the effect of declining daylength at the end of the summer, leads to testis regression. Spontaneous regrowth of the testes, which is independent of daylength, then occurs, and this probably explains why some male wild rabbits begin to regrow their testes at the end of November (Henderson 1979; Davies & Myhill 1980). Therefore, these experimental results help to explain the timing and length of the breeding season in wild rabbits.

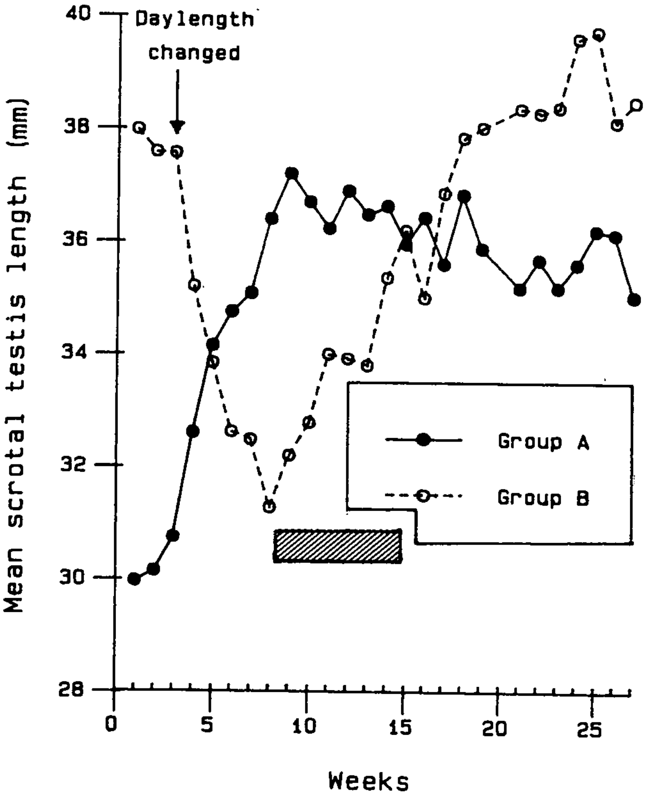


Figure 63 The mean testis length of adult male wild rabbits transferred from short (8L:16D) to long (16L:8D) daylengths (group A) and from long to short daylengths (group B). The time of moult in group B is shown by the hatched bar

I L Boyd

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Programme 9
PLANT POPULATION ECOLOGY

DEMOGRAPHIC GENETICS OF THE PERENNIAL HEATHLAND GRASS *AGROSTIS CURTISII*

Evolution can be perceived in many ways, including the transformation through time of the genetic composition of populations of a species, primarily under the influence of natural selection. This transformation is best studied 'longitudinally', ie by analysing the genetic composition of each generation as it appears, and interpreting changes between generations in terms of the relative roles of natural selection, chance, mutation and migration. In practice, however, empirical studies of evolution in plant populations are usually restricted to analyses of populations at one point in time (cross-sectional analyses), with inferences then being drawn from the pattern of variation. For example, correlations may be sought between genotypic and environmental variation, providing indirect evidence of selection. Although it has rarely been possible to determine the age of individuals within a population and to compare the genetic composition of different age classes, as done by Schaal and Levin (1976) with the corm-forming herb *Liatris cylindracea* and by Ledig *et al.* (1983) with pitch pine (*Pinus rigida*), a temporal element can be introduced into cross-sectional studies by considering an adult (survivor) population and its seed (unselected) progeny. Unfortunately, such studies involve assumptions which are only valid in some condition, eg if the direction of selection, and immigration and emigration rates remain more or less constant. The *Liatris* data have been used to provide 'compelling' evidence of both heterozygous advantage (Schaal & Levin 1976) and heterozygous disadvantage (Clegg *et al.* 1978). Longitudinal studies, in which genetic changes have been followed in 'natural' populations of plants over a period of years, are rare, the recent work in Australia on the annual weed *Echium plantagineum* being an exception (Burdon *et al.* 1983). Longitudinal studies of perennial plants have been confined to agricultural stands (eg *Lolium* and other grass species in the sown sward (Charles 1961)), and very few experimental populations (eg white clover (*Trifolium repens*) (Ennos 1981)). Perennial species are likely to have demographically complex natural populations with uneven age structures, viable seed banks, overlapping generations, and possibly highly skewed plant size and fecundity distributions. They therefore present a formidable problem for the analysis of temporal genetic change.

With these considerations in mind, the opportunity was taken to monitor the demographic and genetic changes in a population of the perennial heathland grass *Agrostis curtisii* (formerly *A. setacea*) colonizing heathland on Hartland Moor, Dorset, following a fire which in late August 1976 completely destroyed surface vegetation cover over a large area and exposed mineral soil in several places where the overlying peat was burnt. The post-fire recovery, at least in the study area, was entirely attributed to the establishment of seedlings (for all species). The original aim of the project was to follow the development *de novo* of a population of *A. curtisii* and, by surveying the occurrence of several isoenzymes, to integrate genetic and demographic variables in an analysis of the micro-evolutionary changes as one generation succeeded another.

An area, 4 m × 10 m, was divided into 10 contiguous 2 m × 2 m quadrats, and marked with angle iron stakes and small pegs. This procedure enabled them to be located and accurately mapped each year, using a 1 m metal frame divided into 100 squares, each 10 cm × 10 cm. The first appearance (birth), size and, where appropriate, flowering performance, and death of each plant within the experimental area have been recorded. Maps were drawn in August or September of each year; they reflect the outcome of changes during the previous 12 months, including plants recruited in the autumn of the previous calendar year and the spring of the current year; for example, plants recruited in autumn 1979 and spring 1980 formed the 1979-80 cohort. More frequent monitoring in the early stages indicated that recruitment was almost exclusively by autumn germination: seedlings germinating in spring usually succumbed to the effects of drought.

Three to four bright green leaves were removed per plant for electrophoresis. To minimize the possible effects of partial defoliation, only those plants with 15 or more leaves were analyzed – the decision to ignore the smaller plants was to have important consequences (see later). The leaves were crushed in a Tris-Citric acid buffer (pH 7·2) containing 2-mercaptoethanol, and the crude extract absorbed on to small paper wicks. These wicks were inserted into slits on horizontal starch gels, which were 'run' at 200 V for 20 minutes before the wicks were removed. Electrophoresis was then continued for 3-4 hours. The gels were routinely assayed for 7 enzymes whose isoenzymes regularly gave consistent, easily scored and repeatable results, and which crossing experiments had established were controlled by Medelian genes (*A. curtisii* is diploid and an obligate outbreeder (Gray & Bates 1979)). The 7 enzymes were Glutamate oxaloacetate transaminase (EC no. 2.6.1.1) *Got*, Phosphoglucose isomerase (5.3.1.9) *Pgi*, Shikimic dehydrogenase (1.1.1.25) *Shdh*, Acid phosphatase (3.1.3.2) *Acph*, Esterases (3.1.1-) *Est*, Peroxidases (1.11.1.7) *Per*, and Superoxide dismutase (or Tetrazolium oxidase) (1.15.1.1) *Sod*; electrophoretic details and staining methods will be published elsewhere. A total of 9 loci have been identified and designated as follows: *Got* 3, *Pgi* 3, *Shdh* 1, *Acph* 5, *Est* 2, *Per* 1, *Per* –1, *Per* –3 (numbers referring to zones of activity on the appropriate gel). Three *loci* (*Got* 3, *Pgi* 3 and *Shdh* 1) contain 3 alleles (labelled a, b and c in order of mobility), all others being diallelic. Heterozygotes of *Got* 3 and *Pgi* 3 were triple-banded, indicating dimeric enzymes; 'null' alleles were present in the cathodally migrating Peroxidase loci. The variation in the *Sod* isoenzymes has not been analysed, despite the occurrence of 4 easily scored and reproducible bands.

The annual records show that the population reached a peak (563 individuals) in 1980, 4 years after the fire (Figure 64). Since then, it has gradually decreased as ericaceous species, principally *Erica cinerea* and *Calluna vulgaris*, have come to dominate the vegetation. Recruitment in the late autumn following the fire is

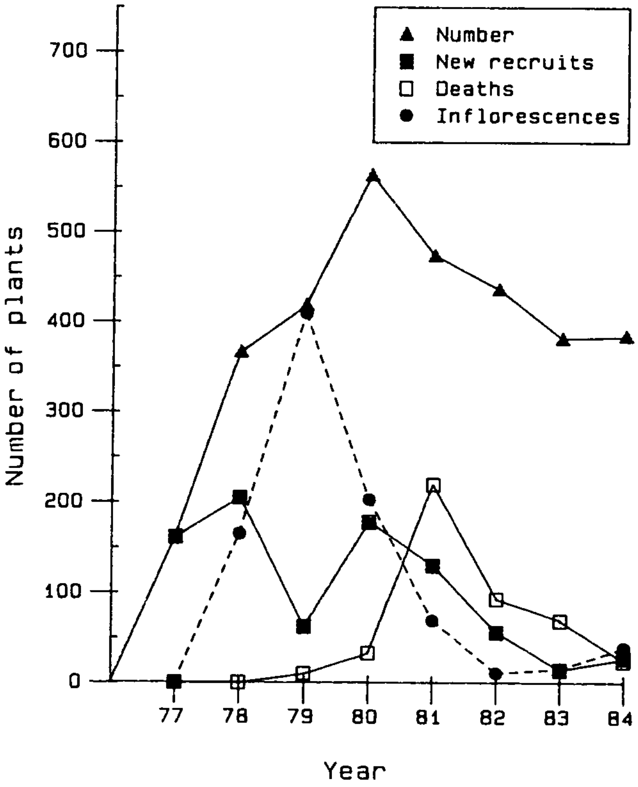

Figure 64 Changes in the population of Agrostis curtisii *colonizing an area of Hartland Moor burnt in August 1976*

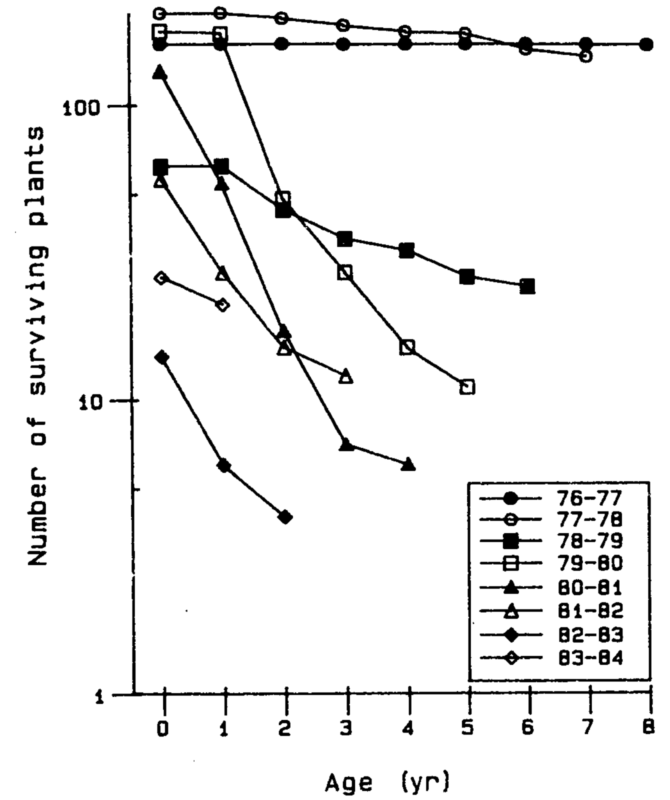

Figure 65 Survivorship curves for each cohort of Agrostis curtisii *colonizing Hartland Moor since it was burnt in August 1976*

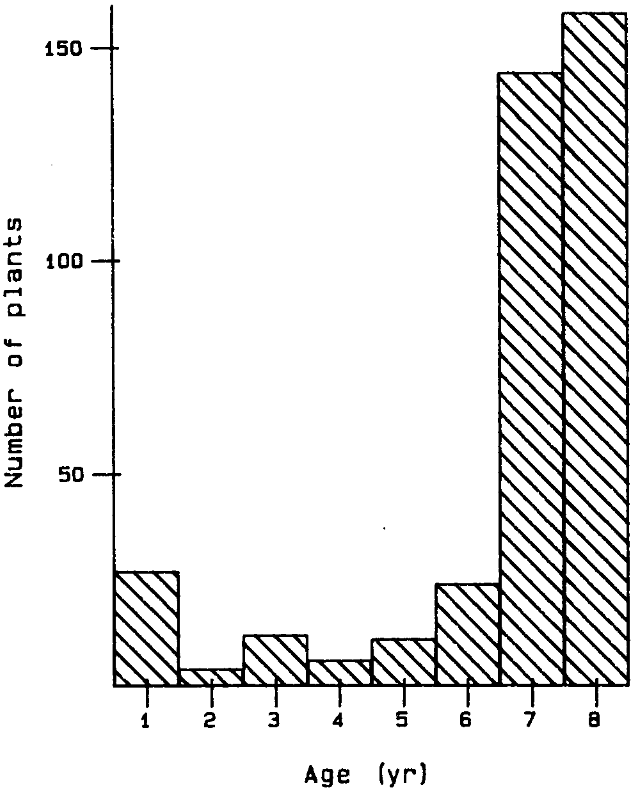

Figure 66 Age structure in 1984 of the population of Agrostis curtisii *that colonized an area of Hartland Moor burnt in August 1976*

thought to have been from seed of surviving plants in nearby firebreaks and hedgerows, and, to a lesser but unknown extent, from seed banks in nearby unburnt soil. Recruitment was erratic over the first 4 years, but the peak in 1980 follows the peak in flowering the previous year when the pioneer cohort, 1976-77, produced more than 4000 inflorescences – an estimated 10^6 seeds (Gray & Bates 1979). The sharp rise in death rate in 1981 was largely caused either by the death of individuals recruited in 1979-80 (57% of those which died) or individuals which had germinated and died since the 1980 census (34%). The survivorship curves for individual cohorts (Figure 65) indicate that very few deaths occurred among plants recruited during the first 2 years after the fire, when the site was mostly bare with scattered seedlings of *Calluna vulgaris, Ulex minor* and *Erica* species (as well as *A. curtisii*). Only 3 of 161 plants in the 1976-77 cohort had died by 1984. In contrast, few of the individuals of post 1978-79 cohorts have survived, eg the 1979-80 cohort has been reduced from 174 to 11 plants in 4 years. The net effect of this pattern of survival was the production of a population with a very uneven age structure (Figure 66), dominated by individuals from the 2 oldest year classes. Not only do these individuals dominate numerically, but they are also the largest and most fecund. Only plants recruited during the first 3 years have flowered, and, of the total of 9125 inflorescences produced in the past 8 years, 8877 (97·3%) were from the 1976-77 cohort and 10 (0·1%) from the 1978-79 cohort. The slight resurgence of flowering since 1982 (Figure 64) is attributable to a second burst of flowering in the 8-year-old plants. Plants recruited after 1979 are typically small, in addition to being non-flowering. Most have only 2 or 3 leaves; only 6 individuals have become large enough to sample for electrophoresis. Hidden beneath the canopy of *Erica cinerea* and other tall plants, such individuals of *A. curtisii* are remarkably persistent. The demographic structure of the population of *A. curtisii* implies that recruitment to the sexual population has effectively ceased, or will be a rare event. Selection, if it occurs, will be by the gradual genotype depletion of the founder population, composed principally of the cohorts of 1976-77 and 1977-78. A similar situation has been described among populations of pasture grasses (see Charles 1966). The turnover of generations, required for the longitudinal study of genetic change through time, has not occurred. This failure and the decision not to sample small individuals have thwarted attempts to compare gene and genotype frequencies in different cohorts.

If the colonists are not being replaced, does their spatial distribution suggest that natural selection was involved during their establishment phase? At the ecological level, analysis of pattern using the variance/mean ratio (see Kershaw 1964) suggests a non-random contagious distribution at a block size which suggested that seeds from the same panicle commonly germinated close to each other, or that small 'safe sites' for germination were widely scattered. Know-

Table 19. The nature of the recuitment site (as defined by plant species within 1 cm of seedlings of *A. curtisii*) and fate of the individuals within the 1978-79 cohort of *Agrostis curtisii* colonizing an area of Hartland Moor burnt in August 1976

	Nature of recruitment site				
	Ulex miñor	*Erica cinerea*	*Calluna vulgaris*	*Agrostis curtisii*	Bare ground
Number of *A. curtisii* recruits in 1978-79	34	9	4	1	14
Number of *A. curtisii* 1978-79 recruits surviving	16	3	0	0	4
% survival (survivorship)	48·5	33·3	0	0	28·6

ledge of the site of recruitment and fate of all individuals in the 1978-79 cohort suggests that survival was non-random (Table 19). Seedlings associated with *Ulex minor* grew faster and had a higher survivorship (persisted longer) than those at other sites – possibly an effect of the nitrogen-fixing properties of that species. A disproportionately large number of plants was recruited at *Ulex minor* sites in relation to the cover of that species in the quadrats. Several factors may have contributed to this recruitment, including the ease with which young gorse plants will trap seed or panicles blown across the open heath, and the possible protection they afford from grazing. Conversely, other species may have had inhibitory effects.

At the genetical level, the survey of variation among 9 enzymes has shown how the population is structured. There are several problems associated with the definition, and the empirical detection, of a genetically differentiated population (Crawford 1984). However, in a population with random matings (panmictic), the frequency of different genes and genotypes should not differ significantly in different parts of that population. However, in the Hartland population of *A. curtisii*, there are significant differences – the allele frequencies, except that of *Per* −2b, in the sub-populations found within the southern half of the experimental quadrat differed from those in the northern half (Table 20) (maps of the distribution of 2 loci are given by Gray and Ambrosen (1982)). There are many possible reasons for this difference. For example, non-random spatial arrangements of genotypes may arise simply because of the limited mobility of pollen and reproductive propagules. However, it is particularly interesting to note that the pattern of variation in the Hartland population matches the geographical distribution of allele frequencies in *A. curtisii.* A survey of 30 populations (comprising 100 plants from 5 populations in each of the 6 regions: Surrey, Purbeck, Dartmoor, Exmoor, south Wales and west Cornwall) has revealed

Table 20. The heterogeneity of allele frequencies in the southern and northern halves of a population of *Agrostis curtisii* at Hartland Moor, Dorset

Locus/allele	Heterogeneity in southern population	Heterogeneity in northern population	Significance of difference between southern and northern populations
Est 2a	·28	·51	***
Per 1b	·12	·15	*
Per −3a	·64	·74	**
Per −2b	·52	·58	NS
Per −1b	·32	·56	***
Got 3a	·13	·18	***
b	·49	·64	***
c	·37	·18	
Pgi 3a	·28	·29	
b	·34	·27	***
c	·38	·44	
Shdh 1a	·16	·12	
b	·65	·55	***
c	·19	·33	
Acph 5c	·27	·61	***

*, **, *** Significant at P = 0·05, 0·01 and 0·001 respectively
NS Not significant

For each locus $\chi^2 = 2N\left(\sum_{j=1}^{k} \frac{6^2P_j}{\bar{p}_j}\right)$ where P = allele frequency
N = total number of individuals
$\bar{p}$ = weighted mean allele frequency
k = number of alleles

(Snedecor & Irwin 1933)

clinal patterns of allele frequency distributions with the frequency of *Got* 3a, *Pgi* 3c, *Shdh* 1c, *Acph* 5c, *Est* 2a, *Per* 1b, *Per* −1b, *Per* −2b, and *Per* −3a increasing in a westerly direction. All but one of these alleles has significantly higher frequency in the northern, than in the southern, part of the Hartland quadrat. The slope of the ground from south to north in this quadrat suggests that the northern section might have been considerably wetter during the period of colonization – indeed, several weeks of heavy rain followed the drought of 1976 and pools of water were to be found during the autumn.

The correspondence between geographical and extremely local patterns of allele frequency distribution leads to the hypothesis that some aspect of soil water level or moisture may be an important selective force, recognizing that variation in heritable factors may reflect indirect effects operating through linked characteristics. Nevertheless, pairs of closely adjacent populations in comparatively wet and dry habitats are currently being screened electrophoretically to see if the 'Hartland pattern' is repeated or is simply fortuitous. At present, there are no clear relationships between isoenzyme variation and plant performance, eg between levels of heterozygosity and flowering. Despite sub-population heterogeneity, growth and fecundity differences between plants within the quadrats appear to depend more on year of establishment and local micro-site differences than on position along the north/south slope. This observation suggests that factors other than those influencing the establishment of the seedling population are now operative. The difference between factors operating during establishment (viability selection) and later performance and survival (fecundity selection) highlights the need to consider the different phases of a species' life cycle when empirically studying plant evolution.

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THE DEMOGRAPHY OF THE BEE ORCHID

The population ecology and demography of 3 terrestrial orchids, autumn lady's-tresses (*Spiranthes spiralis*), man orchid (*Aceras anthropophorum*) and musk orchid (*Herminium monorchis*), have been studied at chalk grassland sites in Bedfordshire since 1966 (Wells 1981). This study, using co-ordinates to identify individual plants (Wells 1967), was extended in 1979 to include a population of bee orchids (*Ophrys apifera*) within a 10 m × 10 m plot on a heavy clay soil at Monks Wood. This population has steadily increased from 66 individuals to 468 in July 1984 (Figure 67). The recruitment of new plants has varied between 42 in 1983 and 226 in 1984 and, except in 1983, numbers of

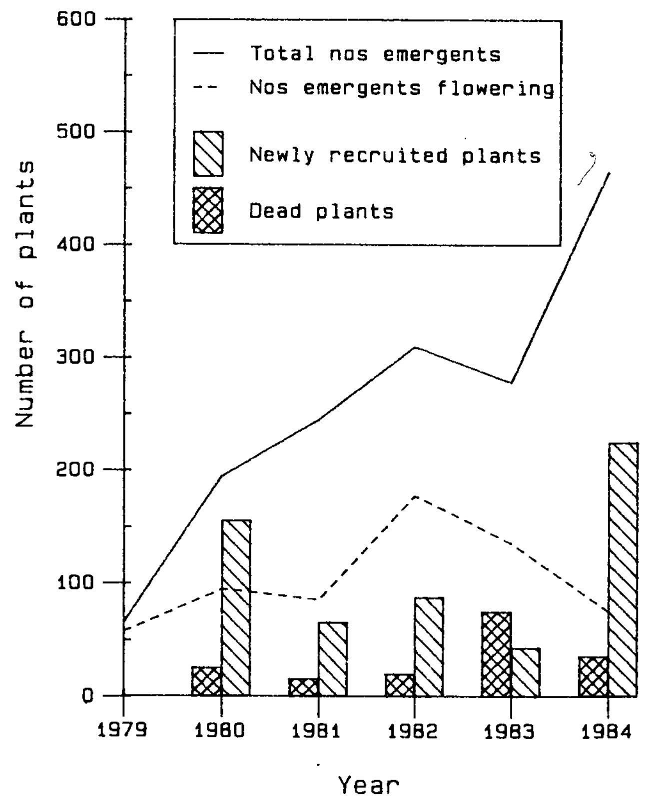

Figure 67 Changes in the numbers of bee orchids within a study area 10 m × 10 m at Monks Wood

Table 21. The frequency of flowering among bee orchids joining a population in different years between 1979 and 1984

Years in which plants were first observed (cohorts)	Number of years in which individual plants were observed flowering 0	1	2	3	4	5	6	Total number of plants in the different cohorts
1979	0	2	19	15	5	1	0	42
1980	5	27	64	34	4	3	–	137
1981	3	10	19	7	2	–	–	41
1982	3	13	12	1	–	–	–	29
1983	14	9	0	–	–	–	–	23
1984	20	4	–	–	–	–	–	24

Table 22. Numbers and sizes of leaves in flowering and non-flowering bee orchids (observations are means of at least 100 replicate plants)

Date of observations	Observations related to plants that were to flower (F), or remain vegetative (V) in June 1983	Mean length (cm) of longest leaves	Mean number of leaves
Nov 1982	F	4·22 ± 0·17	1·87 ± 0·06
	V	2·86 ± 0·15	1·05 ± 0·05
Mar 1983	F	5·32 ± 0·11	2·99 ± 0·04
	V	3·94 ± 0·12	1·97 ± 0·06
May 1983	F	Not recorded	4·70 ± 0·08
	V	Not recorded	2·84 ± 0·08

recruits have appreciably exceeded mortalities. Contrary to Summerhayes' (1951) description, most plants flower in more than one season (Table 21).

The leaves of bee orchids in the Monks Wood population begin to emerge in September, to become moribund at flowering the following June. On other soil types, for example gravelly soil, leaves may blacken and die in March-April in response to drying winds and/or drought. The length of the longest leaf, and the numbers of leaves per plant were measured as indicators of leaf area and plant performance. Plants which flowered the succeeding June had significantly larger leaf areas than plants which did not; the difference was already significant in late October (Table 22).

In order to study this relationship between plant size and flowering, tuber and inflorescence development was studied in an adjacent population which was destructively sampled on 4 occasions between November 1983 and June 1984. Inflorescences less than 5 mm long were detected in the November sample of the large plants, each inflorescence having an average of 6·0 flower primordia. However, in June, there was an average of only 3·1 flowers per inflorescence indicating that many flowers abort during development, presumably because at least one of several possible resources is limiting. In the permanent plot, mean numbers of flowers per inflorescence ranged from 2·6 in 1984 to 3·7 in 1982 when most plants flowered.

At flowering (Plate 28), plants of the bee orchid have (i) 'empty' tubers, which earlier in the year provided nutrients for the current year's inflorescences and foliage, (ii) a large solid, white tuber from which leaves are produced in September, and (iii) an inflorescence. The new tubers usually arise as small white protuberances in November from a stem lateral bud, slightly above the existing tuber. The protuberances increased in size slowly until March (the end of winter); thereafter, their development accelerated, as happens with the man orchid (Wells 1981). As might be expected, for large plants, of similar size, the development of an inflorescence reduced the size of the new tuber (Plate 29).

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HOW IMPORTANT ARE BANKS OF BURIED SEEDS IN THE CAIRNGORM MOUNTAINS?

In treeless habitats within the forest zone, large numbers of seeds can remain dormant in soil for long periods (Roberts 1981); buried viable seeds have also been found in the tundra (McGraw 1980). In the Cairngorm Mountains, the cold temperatures that prevail above the tree line might reduce germination, predation and decay, and so lead to the persistence of a stock of viable seeds buried in the soil. In an environment where annual seed production by many plants is both sparse and erratic (Miller & Cummins 1976), such a persistent seed bank could facilitate plant establishment on disturbed ground.

Beginning in summer 1980, before the new season's seeds had been shed, soils from the Cairngorms were examined for their loads of viable seeds – samples were taken from 9 plant associations (described by McVean & Ratcliffe 1962) occupying large blocks of land above an altitude of 650 m. New inputs of seeds were measured for one year, starting from May 1981.

Numbers of seed-bearing species, of new seeds shed, and of old seeds stored in soil all decreased with increasing altitude, between 650 m and 1200 m (Table 23). Viable seeds were found in all soils in numbers that broadly reflected the amounts shed in 1981-82 (rank correlation coefficient +0·73, $P<0·05$). Seed banks were particularly large where heather (*Calluna vulgaris*) was a dominant element of the vegetation assemblage. One stand of damp heather moor at 680 m had 101 000 buried viable seeds m^{-2}, 95% of them heather. Close to the upper altitudinal limit of heather, soil carrying dwarf *Calluna* heath averaged 11 000 buried seeds m^{-2}. Stocks of buried viable seeds were generally small in plant associations above about 850 m, where heather was no longer predominant. Under most of these high altitude associations, soils usually had only a few hundred seeds, while some were bereft. However, exceptionally, soils with stands of wind-swept *Juncus trifidus* heath sometimes had one or two thousand buried viable seeds.

Where heather was the dominant living plant, it was also the main contributor to seed deposits and banks of buried seed (Figure 68). Other dwarf shrubs, notably bilberry (*Vaccinium myrtillus*) and mountain crowberry (*Empetrum hermaphroditum*), were important constituents of seed banks at altitudes of 850-1000 m, while sedges and rushes were the most important contributors to seed banks at 1000 m and higher. Buried seeds of dicotyledonous herbs were scarce or absent everywhere, so reflecting their rarity in the extant assemblages of vegetation. In contrast, very few viable seeds of grasses, particularly mat-grass (*Nardus stricta*) and wavy hair-grass (*Deschampsia flexuosa*), were detected, although these species were common in the standing vegetation of most associations.

Differences in numbers of stored seeds did not directly reflect comparable differences in rates of deposition, because losses of seeds were greater at low altitudes. For example, 75% of heather seeds stored at 715 m lost their ability to germinate within one year, whereas at 815 m the annual loss was only 17%. In 5 of the plant associations examined, the densities of buried viable seeds exceeded the annual densitites of seeds being newly deposited. Although circumstantial, this evidence suggests that the seeds of some species, particularly *C. vulgaris*, may remain viable in soil for many years, perhaps several decades.

While seeds can remain viable in soil for appreciable periods, are they able, on germinating, to add to the numbers of established plants, particularly at high altitudes? Soils were collected in November 1979 from heather-dominant vegetation, one aliquot being sterilized by irradiation while the other was left unsterilized. Pots of the sterilized and unsterilized soils were put out among heather-dominant vegetation on hills at altitudes of 370 m, 580 m and 860 m. Seedlings that grew on the sterilized soils were to be attributed to freshly shed seeds whereas, on the unsterilized soils, they were derived from recently shed seeds and from the pre-existing seed bank.

On the unsterilized soils, fewest seedlings developed at the highest site, 860 m (Table 24). In September 1980, seedling numbers were similar at all sites below 600 m, suggesting that these initial populations had been determined by the size of the seed bank rather than by local conditions. Similarly, winter mortality (41-58%) between September 1980 and May 1981 did not vary much at the 2 lowest sites, 370-580 m, but

Table 23. Numbers of seeds (10^3 m^{-2}), and numbers of species represented, in (i) the annual deposits of seeds and (ii) the accumulations of viable seeds in soils with different plant assemblages at different altitudes in the Cairngorm Mountains

Plant association†	Altitudinal range (m)	Mean number of seed-producing plant species	Buried viable seeds in 1980		Seeds shed in 1981-82	
			Mean number of species	Mean number of seeds	Mean number of species	Mean number of seeds
Alpine *Nardus* grassland	1040-1220	4·3	0·3	0·21	0·2	0·30
Rhacomitrium heath	1000-1220	4·1	0·3	0·21	0·2	1·4
Juncus trifidus heath	940-1230	4·9	1·1	0·90	0·2	0·10
Nardus-Trichophorum snow-bed	890-1000	8·1	1·3	0·70	0·2	0·10
Vaccinium-Empetrum heath	850-1000	6·9	0·9	0·64	0·2	2·1
Dwarf *Calluna* heath	710-920	5·0	1·6	11	1·0	2·2
Damp heather moor	680-815	8·7	2·0	65	1·8	18
Calluna-Eriophorum bog	660-790	7·0	2·0	29	1·0	18
Dry heather moor	680-750	8·1	1·7	39	1·8	119

† Nomenclature follows McVean and Ratcliffe (1962)

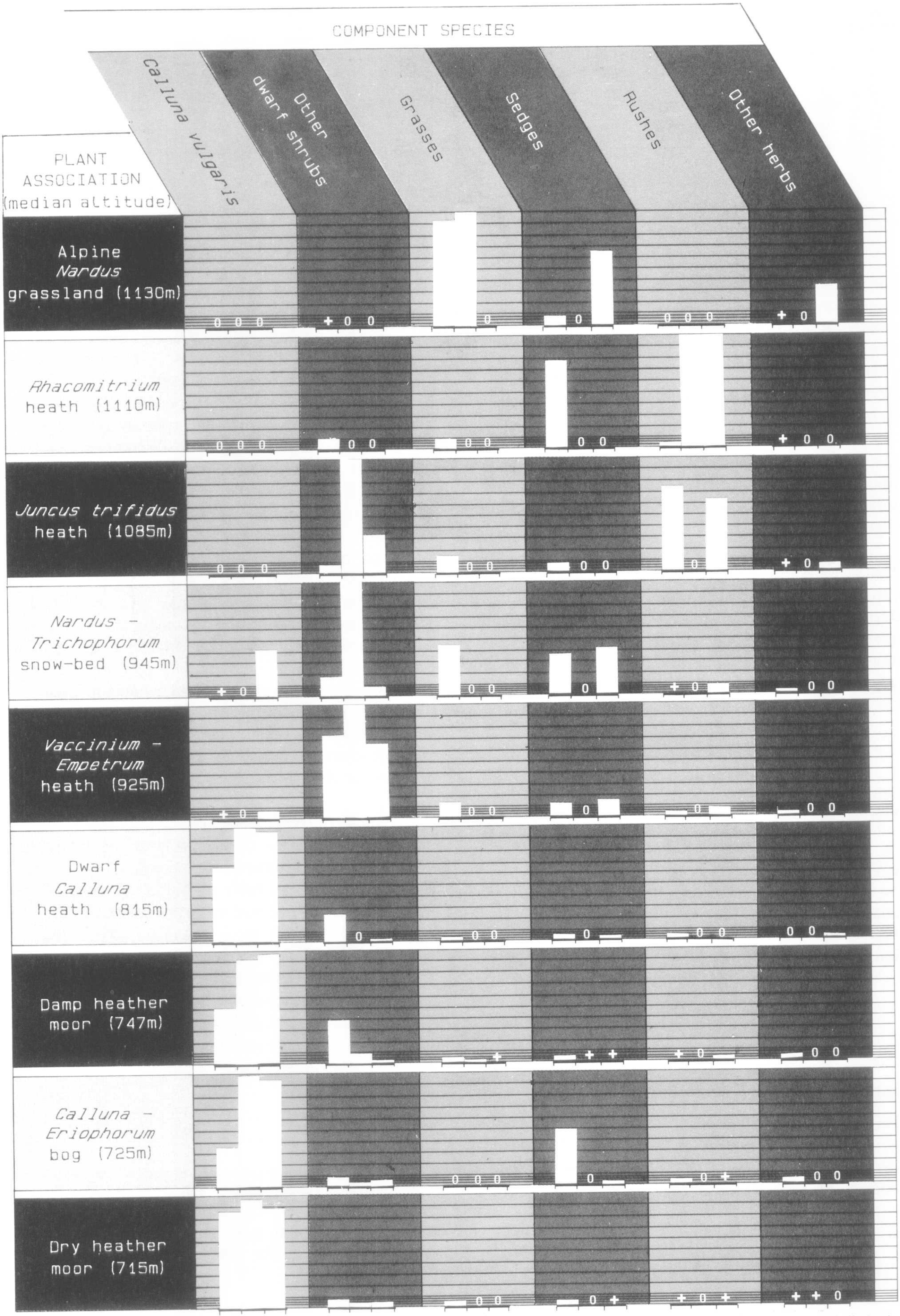

Figure 68 Relative contribution of different species to (i) total cover of seed plants (left bar), (ii) seed fall during 1981-82 (middle bar), and (iii) population of buried viable seeds in 1980 (right bar) in 9 common plant associations at altitudes above 650 m in the Cairngorm Mountains

Table 24. Effects of altitude and local seed source on mean numbers of seedlings emerging from a moorland soil

	Seedlings attributable to recently shed seeds and buried viable seeds			Seedlings attributable only to recently shed seeds
Altitude (m)	Sept 1980	May 1981	Nov 1981	Nov 1981
370	33	14	52	27
580	27	16	24	6·5
860	14	2·5	4·1	0

was significantly greater (82%) at 860 m. Thereafter, during the second growing season, numbers of seedlings at sites at 370 and 580 m, presumably with ample supplies of newly shed seeds, increased substantially, while at 860 m, in the absence of plentiful supplies of new seeds, numbers of seedlings increased by only 2 per pot.

Two years after being set out, the sterilized soils at 860 m were still without seedlings (Table 24), a reflection of the poor seed production by vegetation at that altitude.

This investigation has shown that montane seed banks can be large in relation to the numbers of seeds newly deposited each year. They provide a secure supply of seeds for further recruitment, to compensate for severe seedling mortality during the first winter after germination: a loss attributable to wind-blast and frost-heave.

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POPULATION STUDIES ON ANNUAL LEGUMES

The factors responsible for maintaining species diversity in plant communities were reviewed by Grubb (1977), who identified 5 mechanisms not involving the process of regeneration:

i. variation in life form;
ii. phenological spread;
iii. fluctuations in the environment;
iv. co-existence in balanced mixtures;
v. differences in competitive ability at different stages of development (physiological age).

The importance of the third of these mechanisms, environmental fluctuations, can be conveniently studied using annual species of the Leguminosae. Several genera with annual species, including vetchling (*Lathyrus*), clover (*Trifolium*) and vetch (*Vicia*), have their centres of diversity in the eastern Mediterranean and the Near East. The annual species are characteristic of plant communities in the Mediterranean lowlands but some extend to the British Isles, the northern limit of their distribution. While rough clover (*Trifolium scabrum*) and Bithynian vetch (*Vicia bithynica*) have southern distributions in Britain, twin-flowered clover (*Trifolium bocconei*) is restricted to south-west England. There is evidence that several British species fluctuate greatly in abundance from year to year, for example long-headed clover (*Trifolium incarnatum* subsp. *molinerii*) (Martin & Frost 1980).

Evidence from 3 sources is being used to build up a picture of the population fluctuations of the yellow-vetch (*Vicia lutea*) which occurs locally along the coast of England and southern Scotland, and which has been chosen for detailed study. These sources include:

1. a study of published and unpublished records, which sometimes contain references to years of exceptional abundance or scarcity;
2. a quantitative analysis of herbarium specimens;
3. a study of the annual difference in populations in permanent quadrats.

While collecting data on the performance of the yellow-vetch, observations are being made on associated species so establishing inter-relations, essential information if yellow-vetch and associated vegetation are to be managed successfully.

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Programme 10
AUTECOLOGY OF ANIMALS

THE ECOLOGY OF KESTRELS IN CONTRASTING HABITATS

Kestrels (*Falco tinnunculus*) are widespread and familiar birds of prey. They occur throughout Britain in habitats ranging from desolate moorland to busy city centres. This report compares the results of 2 separate studies of kestrels, one in the southern uplands of Scotland from 1975-79, the other in east England which started in 1980 and is not yet complete. The study areas were about 350 km apart (Figure 69) and differed in the range and abundance of prey available to kestrels, the density and distribution of nest sites, and the levels of organochlorine pesticides used over the past 20 years. The aims were to compare kestrel diets, numbers and breeding performance, and to identify the factors limiting kestrel density in the 2 habitats. Kestrels virtually disappeared from south-east England during the 1960s and early 1970s, when pesticides were heavily used. Since then, they have increased, but there are insufficient pre-pesticide estimates of breeding density to determine whether they have fully recovered their former status. Comparison of results from England with the relatively unpolluted area in Scotland should indicate if pesticides are still having a significant impact on kestrels in eastern England.

The study areas

The Scottish study was at Eskdalemuir, a large area of recently afforested upland. The plantations were mainly of young conifers and the canopy had not yet closed, so most areas had a thick grass ground cover which provided excellent habitat for short-tailed voles (*Microtus agrestis*), the main prey of kestrels. About 30% of the area was unplanted sheepwalk, and 5% was arable farmland. Kestrels nested mainly in disused crow nests which were built in mature conifers. The latter were found in shelterbelts, or small clumps, mostly in the valleys.

The study in England involves 2 areas some 30 km apart in the east midlands. One is in Rutland, and contains a mixture of arable crops (wheat, barley and oilseed rape), grass leys and rough pasture. There are numerous hedgerow trees and small woods. The other site in the Cambridgeshire fens is intensive arable farmland, growing cereals, potatoes, and sugarbeet. There is virtually no pasture and few trees or woods. Both areas have little ungrazed grassland, apart from that along hedgerows and road verges. Most of the nest sites are holes in trees, though a few are in buildings or strawstacks.

Diet

In both studies, diet was measured by recording the percentage of pellets that contained a particular item in 6 2-monthly periods each year (Village 1982a). At Eskdalemuir, voles were always an important item, usually present in at least 90% of pellets from any 2-monthly period (Figure 70i). Even when voles were scarce in 1977, they still occurred in more than 80% of kestrel pellets. Other prey included shrews, small birds, beetles and earthworms. These items were taken mainly when they were seasonally abundant, or if voles were scarce. Small birds, for example, were most frequently eaten in June and July, when the recently fledged young were vulnerable to predation by kestrels (Figure 70ii). It was difficult to identify the species of small birds in pellets, but feathers of kills at nests were mainly meadow pipits, skylarks and starlings. The seasonal peak in small birds was higher when voles were scarce in 1977 than in the other years when voles were more plentiful. Most small

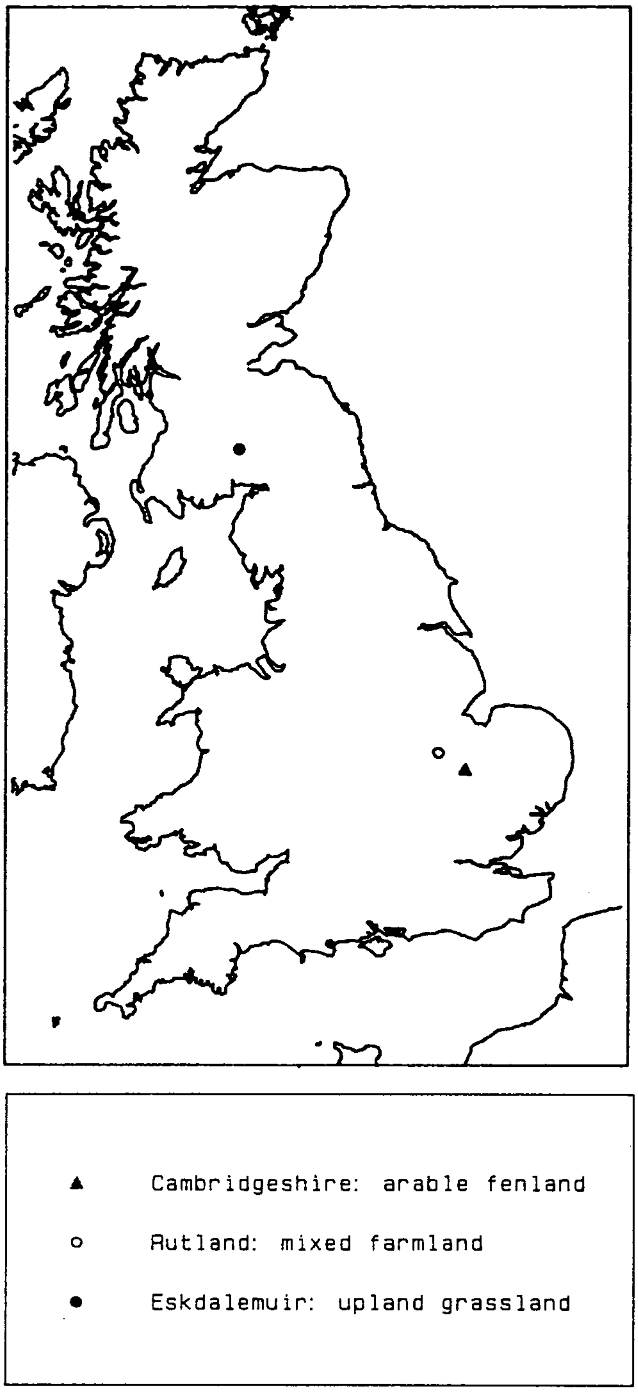

Figure 69 Location of the study areas

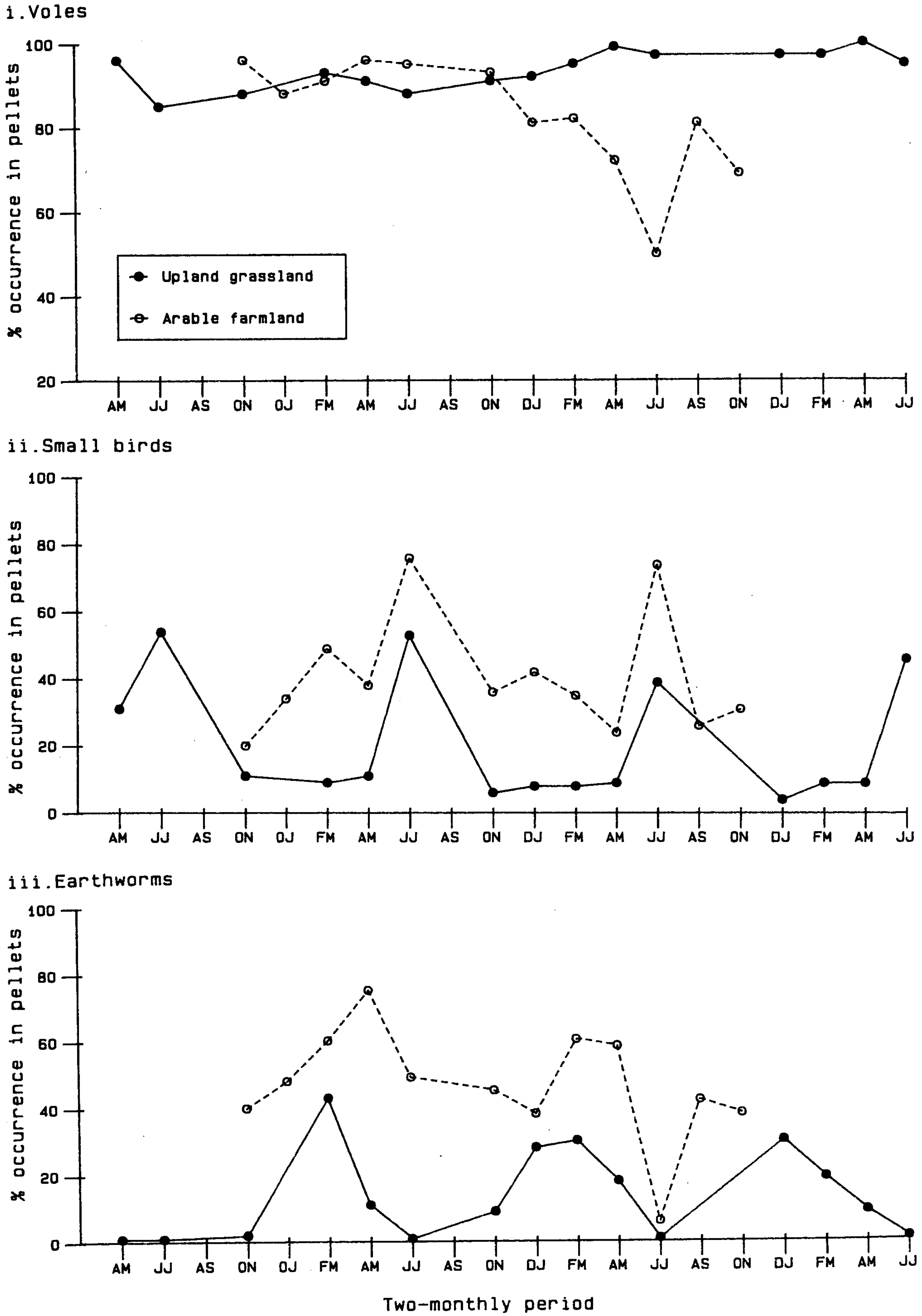

Figure 70 *Comparison of kestrel diets in upland grasslands in Scotland (1976-79) and arable farmland in England (1981-82). Each point is based on the analysis of about 100 pellets and is the percentage of those pellets that contained the item in question*

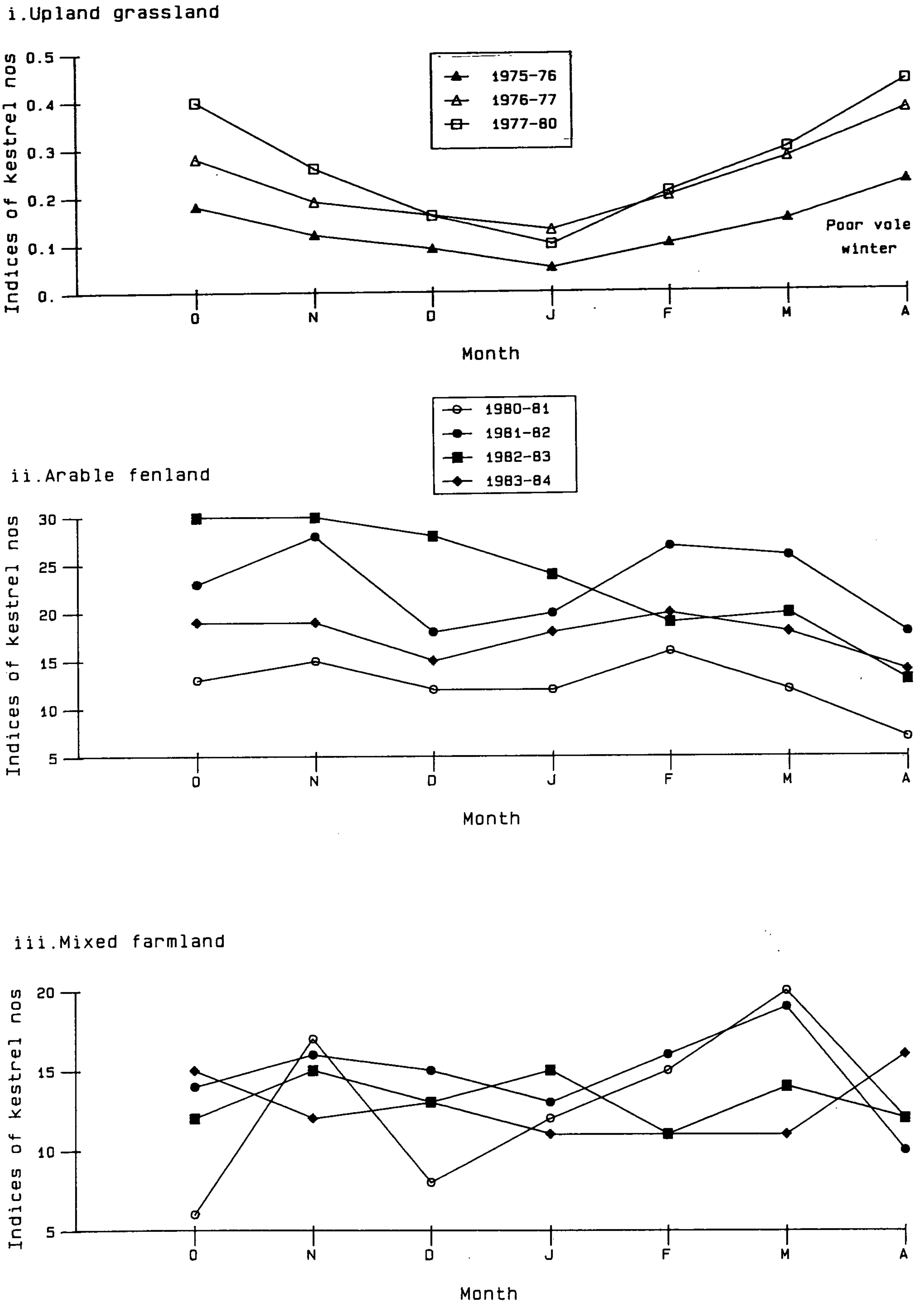

Figure 71 Comparison of winter numbers in the 3 study areas, in different years, based on roadside counts. Kestrel numbers are expressed as indices of abundance that are not directly comparable between the areas. Upland data are from Village 1982b

birds left the hills in winter, so they were rarely eaten by kestrels outside the breeding season. Earthworms were another seasonal item, eaten mainly in early spring (Figure 70iii), when the ground was warm and waterlogged. Earthworms come to the surface in these conditions, and are available to kestrels, particularly where the grass is grazed short.

The few pellets so far analysed from the farmland sites have already indicated important differences in diet compared with the uplands. Voles were again a major prey, but occurred in only half the pellets examined in June-July 1982, when voles were scarce (Figure 70i). Differences in diet were more striking in other items, such as small birds, which showed the same seasonal trends, but were more frequently taken than in the uplands, especially in winter. Farmland kestrels also took a wider variety of species, ranging in size from blackbirds and thrushes to blue tits. Differences were also apparent in other items such as earthworms (Figure 70iii), which again showed the same seasonal peaks as in the uplands, but were more frequent in the diet at all times of year.

The more varied diet of kestrels in farmland than in the uplands probably reflects differences in prey abundance between the 2 habitats. In the rough grassland at Eskdalemuir, voles were the most common prey species, especially in winter when there was little alternative food. In arable farmland, however, there was much less suitable vole habitat, and a greater diversity of other prey species.

The winter population

At Eskdalemuir, winters were fairly harsh with frequent, but not permanent, snow cover. Kestrel pairs separated after breeding and most left the area, probably going south into England, or the continent. By December, all the remaining kestrels occupied individual territories that increased in size as numbers declined (Village 1982b). Seasonal changes in numbers were monitored by counting kestrels from 1976-78 (Figure 71). Within years, numbers usually declined until December or January, and increased thereafter, when migrants arrived in spring. There were significant differences between years and kestrel numbers were lowest in the poor vole winter of 1976-77. Males predominated among the wintering population, especially when voles were scarce (Table 25). First-year birds, however, showed the opposite trend, with fewer present when voles were scarce (Village in press).

Table 25. The percentage of adult male kestrels among the wintering population in 3 habitats. Based on the proportion of sightings of all birds that could be classed as either adult male or female/juvenile male

Habitat	Winter	Percentage of adult males
Upland grassland	1975/76	56
	1976/77	70
	1977/78	27
Mixed farmland	1980/81	36
	1981/82	33
	1982/83	36
	1983/84	33
Arable farmland	1980/81	14
	1981/82	21
	1982/83	18
	1983/84	21

Results from the farmland study suggest a pattern of wintering that is quite different from the uplands. In both farmland sites, but especially in mixed farmland, pairs frequently remained together during the winter and re-mated the following year. Members of pairs usually kept their own hunting space, but met frequently during the day to sit together on the same perch. Numbers were fairly stable during winter and there was less year-to-year variation, especially in mixed farmland (Figure 71). The density of kestrels in the fens in winter seems to be higher than in either the mixed farmland or upland areas, though more work is needed to confirm this fact. The fens are an important wintering site for juvenile and female kestrels, many of which may originate from more northerly parts of Britain, such as Eskdalemuir.

Differences in the age and sex ratios of the 3 populations are reflected in the proportion of adult males present during winter (Table 25). Adult males can easily be distinguished from either females or juvenile males by their plumage. The scarcity of adult males wintering in the fens reflects the greater abundance of females and first-winter birds of both sexes, compared with the mixed farmland or the uplands. More work will be done to find out why this is so.

Breeding density

Breeding density varied considerably, both between the uplands and farmland areas, and between the farmland areas themselves (Table 26). The highest densities were at Eskdalemuir, where the number of breeding pairs varied from 22 100 km^{-2} in 1976, to 37 100 km^{-2} in 1978. These figures do not include kestrels breeding at experimental nest sites in 1978, when the total density of breeding pairs was 45 100 km^{-2}. The density in mixed farmland was more stable between years and was about 70% of that in the uplands. Breeding density was lowest in the fens, being on average only 35% of that in the uplands. This low density may partly have been due to the scarcity of nest sites, because there were few trees, though providing nest boxes has not yet significantly increased the number of pairs in that area.

The regulation of breeding numbers in the uplands involved food supply, nest site availability and territorial behaviour (Village 1983). The usable sites (mainly old crow nests) were found in clumps in each small shelterbelt. When voles were scarce, kestrel territories were large, and the first pair to settle in a wood prevented others from occupying any surplus nest sites nearby. When voles were more abundant, kestrel territories were smaller, and several woods had 2 or more pairs of kestrels, sometimes nesting only a few metres apart. Even in these years, not all kestrels in the area were able to find a nest: kestrels of either sex, removed from their territories late in the season, were replaced by others that bred subsequently. Artificial nest sites made available late in the season, and outside kestrel territories, were occupied by pairs that bred successfully. These pairs clearly had enough food to breed, but would not normally have done so because they lacked a suitable nest site. The shortage of sites was not due to lack of crow nests *per se*, but arose because of the way the kestrels defended their nests. Territory size was itself related to vole abundance, so food supply was probably ultimately, but indirectly, limiting kestrel breeding density.

The mechanism by which breeding density is regulated on farmland is not yet known for certain, but direct food shortage seems to be more important than shortage of nest sites. Removal and 'late-nest' experiments, similar to those in the uplands, have failed to demonstrate the existence of a large, non-breeding surplus of kestrels unable to breed for lack of a nest site. Two females removed from their territories were replaced by first-year birds that subsequently bred with the 'widowed' males. Where males have been removed, however, they have not, so far, been replaced. Males are responsible for feeding their partners from before egg laying until the young are about 10 days old. The lack of male replacements may have been because any non-breeding males in the area were unable to support a female anyway, and any that were able to mate could easily find a nest site and were already paired. If this hypothesis is true, erecting large numbers of next boxes in farmland early in the season should not appreciably increase breeding numbers, which would still be held down by lack of food. This and other experiments are planned for the next few years.

Breeding performance

The idea that food supply is poorer in farmland than in upland grasslands is further supported by differences in the timing and success of breeding between the 2 habitats. Mean laying date in kestrels is related to food

Table 26. Breeding density of kestrels in 3 habitats

Habitat	Area searched	Year	Territorial pairs 100 km^{-2}	Breeding pairs 100 km^{-2}
Upland grassland	100 km^2	1976	30	22
	100 km^2	1977	28	27
	100 km^2	1978	38	37
	100 km^2	1979	36	36
		Mean	33	31
Mixed farmland	108 km^2	1981	32	27
	108 km^2	1982	21	19
	108 km^2	1983	25	21
	108 km^2	1984	22	19
		Mean	25	22
Arable farmland	66 km^2	1981	14	11
	89 km^2	1982	9	9
	89 km^2	1983	16	12
	250 km^2	1984	13	12
		Mean	13	11

Table 27. Mean laying dates and clutch sizes of kestrels in upland grassland in Scotland and arable farmland in east England

Habitat	Year	Mean laying date (SE days)	Mean clutch size (SE eggs)
Upland grassland	1976	30 Apr (1.9)	5.1 (0.2)
	1977	12 May (1.8)	4.6 (0.2)
	1978	28 Apr (1.6)	5.1 (0.1)
	1979	2 May (1.6)	5.1 (0.1)
	All years	2 May (1.0)	5.0 (0.1)
Farmland (mixed and arable fenland)	1981	12 May (2.2)	4.5 (0.1)
	1982	17 May (1.5)	4.2 (0.2)
	1983	13 May (0.9)	4.4 (0.1)
	1984	10 May (1.4)	4.5 (0.1)
	All years	13 May (0.8)	4.4 (0.1)

supply (Cavé 1968), and artificially feeding kestrels can advance their laying dates by several weeks (Dijkstra *et al.* 1982). At Eskdalemuir, laying was about 2 weeks earlier, on average, in the good vole years, than in the poor one (Table 27). Mean laying dates in the farmland areas have so far all been as late as, or later than, the poor vole year at Eskdalemuir (Table 27), despite the fact that the farmland study is further south and at a lower altitude. It seems that the spring food supply in farmland is poorer than most years in the upland grassland. The effect of pesticides on breeding productivity is not yet clear, though any reduction in farmland is probably slight compared with that due to food shortage.

Conclusions

The results so far indicate that the ecology of kestrels in upland grassland and arable farmland differs in several important ways. Food supply on lowland farmland seems to be more stable than in the uplands, partly because of the wider variety of prey available and partly because of smaller year-to-year variations in vole numbers. This, together with the milder winters, results in a stable (and fairly high) wintering kestrel population, with a high proportion of first-year birds. Farmland in eastern England seems to provide suitable habitat for kestrels in winter, when less profitable prey, such as invertebrates or adult passerines, may be sufficient to provide the daily food requirements. During the early breeding season, however, male kestrels feed their partners mainly on voles, and the lack of rough grassland in arable farmland means a poor food supply. As a consequence, kestrels breed at low density, lay late and fledge few young.

Food supply in the uplands is generally unstable, both between years (due to the cycling of vole populations) and from summer to winter (due to the harsh weather and lack of alternative prey in winter). However, the high proportion of good vole habitat in the uplands results in a high breeding density, early laying and good breeding success in all but the poorest vole years.

A Village

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POPULATION STUDIES OF THE ORANGE-TIP BUTTERFLY

The caterpillars of the orange-tip butterfly (*Anthocaris cardamines*) feed on the developing seed heads of a range of cruciferous plants. In Monks Wood NNR, it has only a single food-plant, namely cuckooflower (*Cardamine pratensis*), which is found scattered throughout the wood. The number of *Cardamine* plants flowering varies considerably between years, ranging from an estimated total of 6223 in 1982 to 278 in 1984.

The butterfly makes use of this varying food resource by laying its eggs singly on the opening flower heads. If more than one egg is laid on a plant, the first larva to hatch usually kills the others, so that only one caterpillar per flower head survives. Not all flowers are acceptable to the egg-laying butterfly, and only the biggest, growing in sunny, sheltered rides, are normally laid upon. Survival of the caterpillars through to pupation is better on large flower heads, and at least 4 developing seed pods (siliquae) are needed for a caterpillar to complete its development. Each year many plants fail to produce this number of siliquae (50% 1982; 39.6% 1983; 48.5% 1984).

The impacts on the butterfly's population of changes in the availability of larval food-plants have been considerable. A marked reduction in the numbers of *Cardamine* flowers in 1984 led to very few eggs being laid that year. As far as we can tell, most females emerging in the wood emigrated without laying eggs, and probably fewer than 50 eggs were laid in the whole wood, compared with 800-900 in each of the previous 2 years. Larval survival was also poor in 1984, so we can expect few butterflies, from within the wood, next year.

It remains to be seen whether *Cardamine* will flower next year, and, if it does, whether this will attract butterflies into the wood from outside. The Butterfly Monitoring Scheme (Pollard 1982) has shown that the numbers of orange-tips in Monks Wood have followed those of eastern England over the past 10 years, so it seems likely that the butterfly population in the wood reflects breeding success over a large area, and that dispersal must be quantified if we are to explain the impacts of local food resources on the species.

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DEMOGRAPHIC CONSEQUENCES OF SEXUAL SELECTION IN CAPERCAILLIE

Darwin proposed sexual selection to explain aspects of sexual dimorphism which he could not account for by natural selection. Sexually selected characters may increase a male's mating success, and therefore his total genetic fitness. In theory, this improvement can occur even if the sexually selected character reduces aspects of a male's fitness which are not immediately related to his mating success. Indeed, sexual selection might counteract natural selection to a point where the disadvantages of sexually selected characteristics increase the chances of local populations becoming extinct. The capercaillie (*Tetrao urogallus*) may be an example where this tendency towards extinction has occurred. Although there are many links in the argument which are still speculative, it is worth putting forward because it suggests ideas for future research.

A previous ITE report (Moss 1983) outlined the argument that sexual selection for large sizes in adult cock capercaillie has resulted in a reduced resistance to environmental stress in male chicks. The main evidence was that male chicks suffered heavier mortality than female chicks in years of poor breeding. In a study in Glen Tanar (Moss & Oswald 1985), the number of days with rain in the first 10 days of June, during and just after hatching, was well correlated with the number of chicks reared per hen. Rain in this period, therefore, seems to be the most important environmental stress.

The observation that male chicks survive less well than females in years with long periods of rain in early June can be related to the facts that males are bigger than females, have to grow faster, and require more food. Consequently, they may need to spend more time foraging, and so suffer more when long periods of rain force them to shelter under the hen; also, they may be more easily chilled (Moss 1983).

Although female chicks do survive better than males, they too suffer their heaviest mortality when there are many rainy days in June. If, therefore, female capercaillie were smaller than they actually are, they might survive the rain better.

In many respects, the black grouse is like a small capercaillie. The 2 species are closely related and the young chicks are very similar in general appearance. Both species occur in open, semi-natural pine forest and the production of young by both was recorded in the same study area at Glen Tanar. Despite a clear relationship between the breeding success of capercaillie and rain during and just after hatching, no such relationship occurred with the smaller black grouse. This observation lends support to the idea that the large size of capercaillie contributes to an increased vulnerability of their chicks to the effects of rain. It also suggests the possibility that sexual selection for large size in cock capercaillie has somehow also involved an increase in the size of the hens.

Höglund (1955) argued that the distribution of capercaillie in Sweden was limited by climate, and drew attention to the vulnerability of the young chicks to rainy conditions. This is also one possible explanation of the breeding distribution of capercaillie in Scotland: they breed throughout much of the coniferous forest in the east of the country, but not in the wetter west. Höglund's argument implies that local extinctions of capercaillie are more likely in wetter climates. From the argument on sexual selection outlined above, one can infer that the probability of local extinctions in wetter areas has been increased by the birds' great size, that this size is partly due to past sexual selection, and therefore that one factor limiting the range of capercaillie is the effect on body size of sexual selection.

R Moss

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RESEARCH ON BLACK GROUSE

(This work is largely supported by World Pheasant Association funds)

Numbers of black grouse (*Lyrurus tetrix*) have declined this century in most of western Europe except for Scandinavia. In Britain, the decline is particularly apparent in southern England, where none now breeds. Game bag figures from Scotland also showed a marked drop in most regions in the late 1930s, from which there has been no subsequent recovery.

This ITE study was begun in 1982 and has examined the food and habitat requirements of hens through the year and of broods in summer. It has concentrated on the survival of hens and chicks, as this factor was thought to be particularly important for understanding the decline, and because there had been no recent study of black grouse broods in Britain. Hens were caught and marked with small radio transmitters when they visited the males' display ground (lek) in April. They were then tracked with minimal disturbance, their nests were found, and hens with chicks were located by night. Droppings of hens and chicks were collected from roost sites and analysed to identify items in the undigested fraction of their diet. There are

Table 28. Mean number of arthropods sampled at black grouse brood locations from mid-June to early July 1983, using a sweep net (25 sweeps per sample) in Birse and Glen Tanar, NE Scotland, and breeding performance of unmarked hens there at the end of July in 1983

Size class (mm)	Arthropods Mean number±SD (n samples)		Number of young:1 hen (n hens)	
	Birse	Glen Tanar	Birse	Glen Tanar
2-5	75·0 ± 37·9(14)	139·0 ± 53·3 (6)**	1·6:1 (7)	3·1:1 (13)†
5-10	16·6 ± 11·7	18·7 ± 8.7		
10+	1·1 ± 1.1	3·2 ± 3·4		

** t = 3·06, P<0·01 for the difference between Glen Tanar and Birse

† Data from R Moss (unpublished)

2 contrasting study areas, both in the Grampian Region of NE Scotland: Birse, which is mainly moorland, and Glen Tanar, in which there is a large remnant native pinewood.

The eggs in each clutch hatched synchronously in mid-June, and the chicks left the nest within 24 hours. Broods were then found mainly in grass patches associated with wet flushes on the moor or along streams, in bogs or in forest clearings with bilberry (*Vaccinium myrtillus*) in the ground vegetation. They were rarely found in pure stands of heather (*Calluna vulgaris*), although it was usual for them to roost in long heather close to a feeding area. Most deaths of chicks occurred in the first 10 days, which is the period when chicks, in all the broods studied so far, fed mainly or exclusively on arthropods, and when brood movements (up to 600 m per day) were greatest. The young chicks' diet at this time could be assessed in 2 ways. The most obvious was to analyse droppings, as it was not possible to examine food in the chicks' crops. Droppings collected from roosts in 1982 and 1983 were examined by S Moreby (at the Game Conservancy) and found to contain mainly the remains of ants, beetles (especially the heather beetle (*Lochmaea suturalis*) and weevils), sawfly and Lepidoptera larvae and Ichneumon wasps. Soft-bodied arthropods were probably also eaten, but were digested so completely as to leave no recognizable fragment in the droppings. We have found that hens, both with and without chicks, fed almost entirely on vegetable matter in summer and so did not compete with the young for arthropods.

A second approach was to collect arthropods at chicks' daytime feeding areas. We used a wide-mouthed net of fine muslin to sweep through the vegetation 25 times at each site. All arthropods caught were preserved for later examination. In 1984, in addition to sweep netting, we also used 10 pitfall traps set 1 m apart in a line and left for 24 hours. In 1983, black grouse bred well in the forests of Glen Tanar, but less well on the moorlands of Birse (Table 28). This result was associated with a significantly greater number of small arthropods in Glen Tanar than in Birse (t=3·06, P<0·001, Table 28). The number of larger items in sweep net samples did not differ significantly between the 2 areas.

The total number of arthropods in the samples from both areas was very much greater than that obtained by Savory (1977) from red grouse (*Lagopus l. scoticus*) brood habitats on Kerloch moor, 15 km east of Birse. He used a similar-sized net, but found only 13·3 ± 3·5 SE and 10·0 ± 4·4 SE arthropods per 100 sweeps at the same time of year (the third and fourth weeks of June) in 1969-71. This result implies that habitats rich in arthropods may be even more important for black grouse chicks than has been shown for red grouse chicks (Hudson 1983). If results from 1984 support the suggestion implicit from Table 28 that black grouse chick survival and prey abundance are associated, it may be possible in future to increase experimentally the amount of suitable feeding places for chicks. Improved chick survival could be expected eventually to lead to a recovery in black grouse numbers, at least in some areas.

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THE EFFECTS OF DEPTH ON OTTER FORAGING IN THE SEA

Otters (*Lutra lutra*) are common along the coasts of Shetland (Plate 30). There are also large numbers of fish, and this project is concerned with whether fish populations, or any other resource, may limit the numbers of otters, and, if so, how. The otters are

Plate 27 A mute swan: some 3000-4000 of these birds, representing about 20% of the British population, die annually from lead poisoning caused by ingesting anglers' split-shot lead weights
(Photograph C J Barr)

Plate 28 An individual flower of the bee orchid
(Photograph B Dickerson)

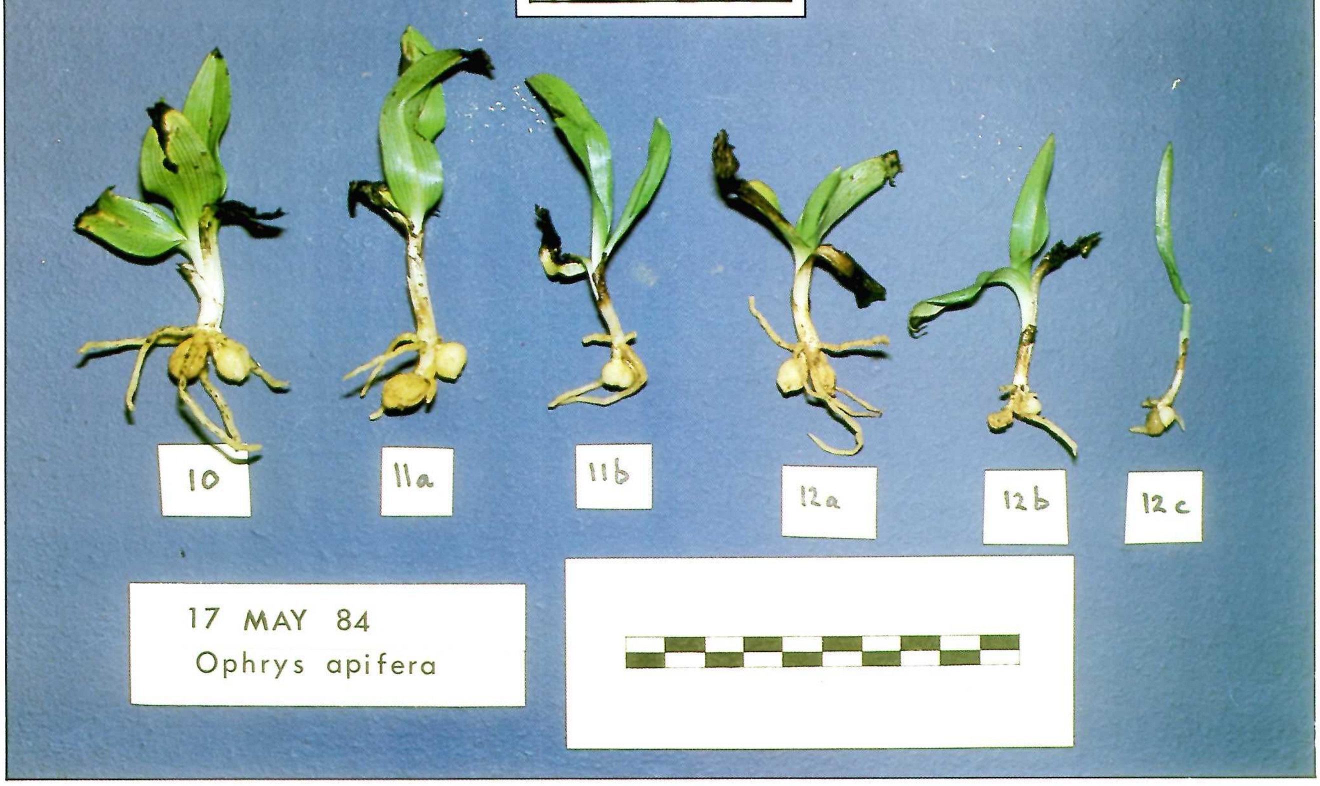

Plate 29 Variation in the size of bee orchids sampled on 17 May 1984. The 'old' tubers which produce the current year's inflorescence are brown and smaller than the white 'new' tubers which will produce next year's inflorescence. The roots are produced annually, in November. All plants except for the smallest (12c) contained an inflorescence, which varied from 23 mm in sample 10 to only 3 mm in sample 12b
(Photograph T C E Wells)

Plate 30 A female otter (Photograph H Kruuk)

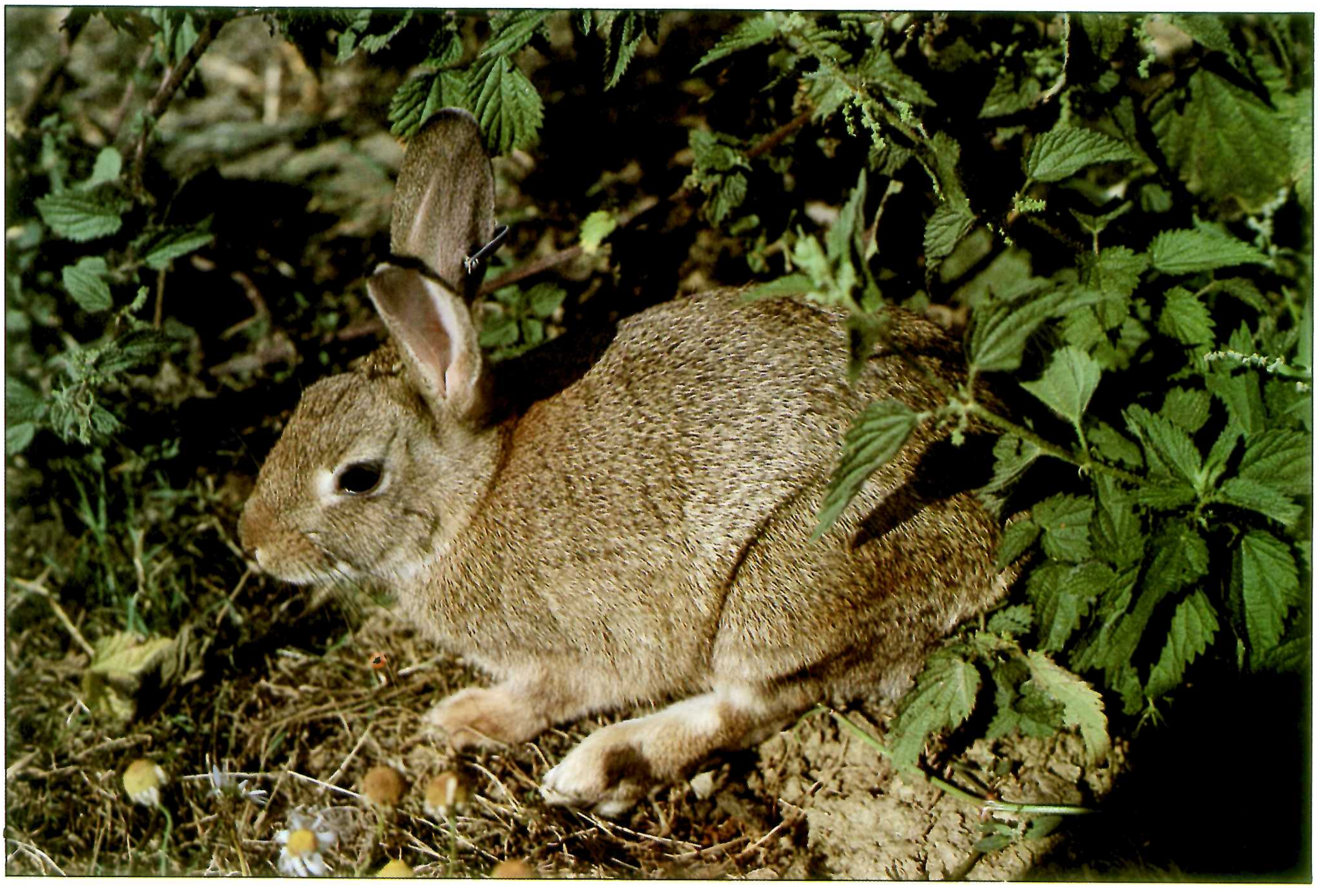

Plate 31 One of the rabbits being studied in the population at Monks Wood (Photograph I L Boyd)

followed, sometimes with the help of radio-location, to determine how they use their habitat, and where and how fish are caught. Most of the prey species caught by otters live on the sea bottom, and this preliminary report describes how the depth of water may affect the otters' foraging effort and their utilization of the coast.

The observations were made in 1983, in the ITE study area, which extends over 8 km of coast and includes 2 bays. The inshore waters were charted in detail, and, each time an otter was seen fishing, the water depth, time spent under water and on the surface, approximate size of prey, and, if possible, the species caught were recorded. Otters fed almost entirely on marine fish belonging mostly to 3 different species, which they ate on the surface. Large fish were brought ashore to eat. The ability of observers to gauge prey size (accuracy over 90%) and species (over 70%) was checked in a control experiment. Once an otter was found, it was followed for as long as possible, often over several kilometres. It could be fishing, ie diving repeatedly in one small area, or swimming on the surface over long distances, or it could be swim-diving, ie covering longer distances with frequent dives. This report describes observations of 1008 dives, made during actual fishing only, between April-September 1983, by about 8 otters, mostly unmarked and without radio-transmitters. Fish populations were sampled extensively, using a funnel trap.

In the bays and a 100 m wide strip along the coast, otters had a clear preference for shallow water (Figure 72): 64% of dives were in water less than 3 m deep, although less than one quarter of the area was that shallow. Such a preference was far less pronounced during swim-diving. This use of shallow water could explain part of the distribution of otter activity along the coast, as there was a correlation between the percentage of each block of the study area under less than 5 m water, and the activity of otters there ($r=0{\cdot}46$, $n=32$, $P<0{\cdot}01$).

The advantage which an otter derives from fishing in shallow water was not immediately obvious, as the success rate of fishing otters increased with depth (Figure 73). However, deep dives also took significantly longer (Figure 74), and the recovery time after a dive, floating on the surface, also became longer with longer dives. The calculated number of fish caught per hour spent under water showed a slight, but insignificant, decrease with depth (Figure 75). Although the number of fish caught per hour under water might be smaller at greater depths, the prey was significantly larger there (Figure 76), indicating an even more dramatic increase in weight of fish caught, as this is a cube function of length. All in all, fishing in deeper water was more productive. However, for a full understanding of profitability of fishing at different depths, estimates are required of the diving effort of otters, and the increase

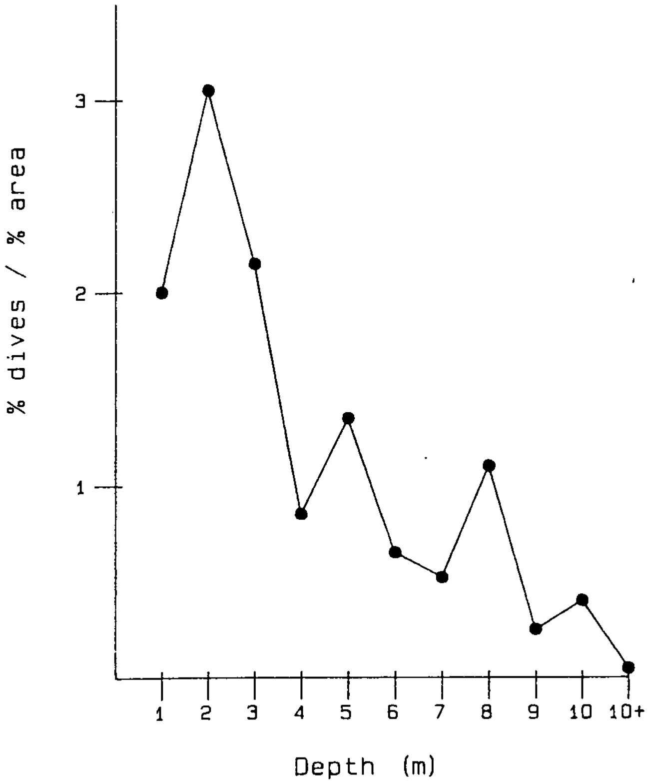

Figure 72 Otters fishing at different depths. The graph shows the percentage of observations of dives for each depth, divided by the percentage of the study area covered by that depth

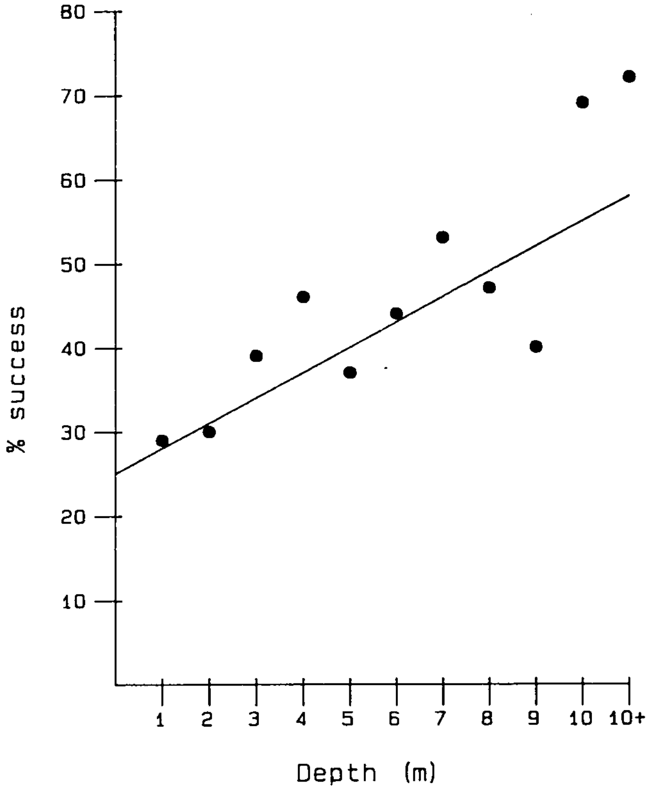

Figure 73 Percentage of dives which were successful, at various depths

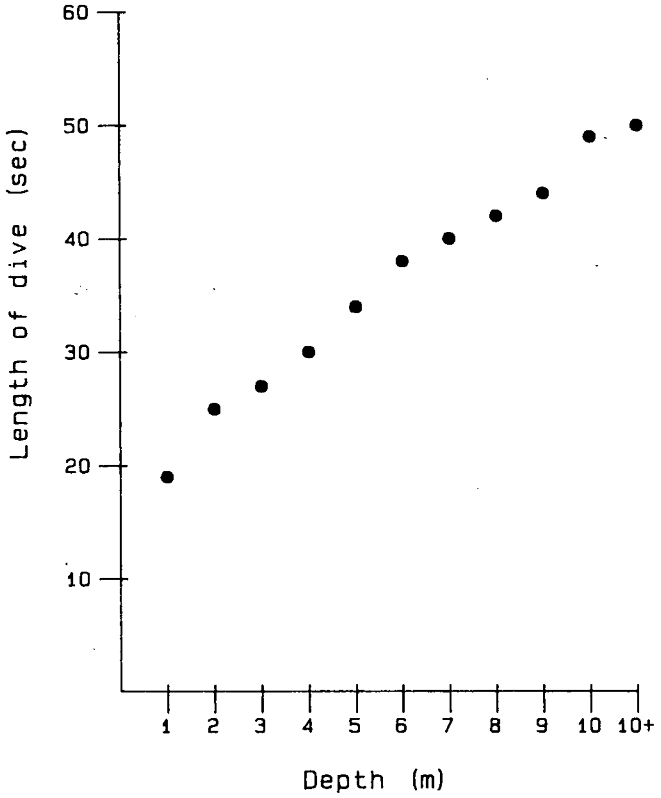

Figure 74 Duration of unsuccessful dives of fishing otters, at different depths

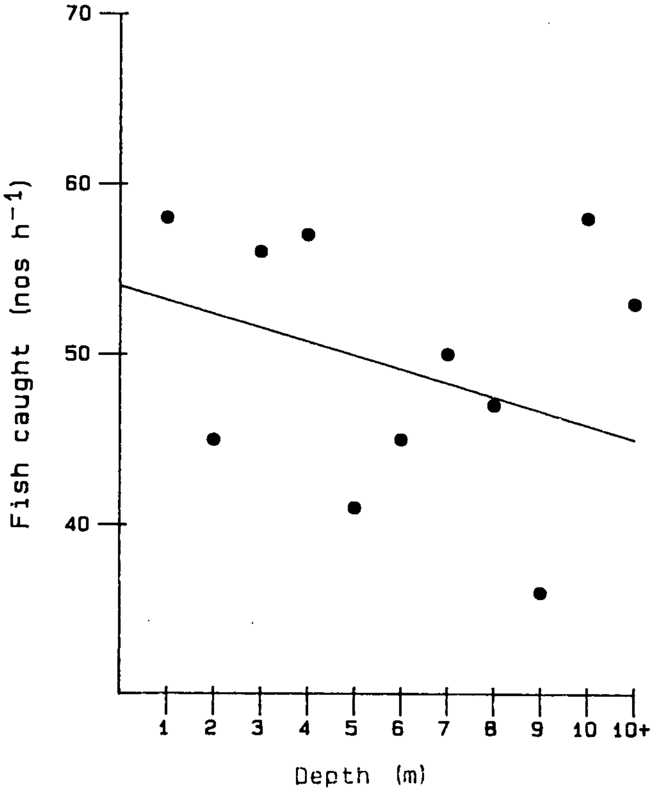

Figure 75 Number of fish caught by otters per hour under water, at different depths

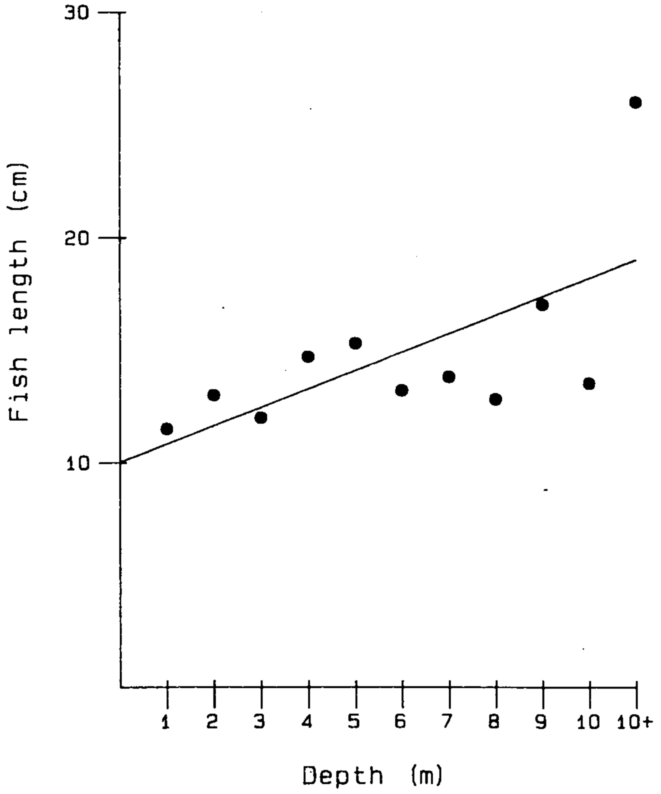

Figure 76 Mean length of fish caught by otters at different depths

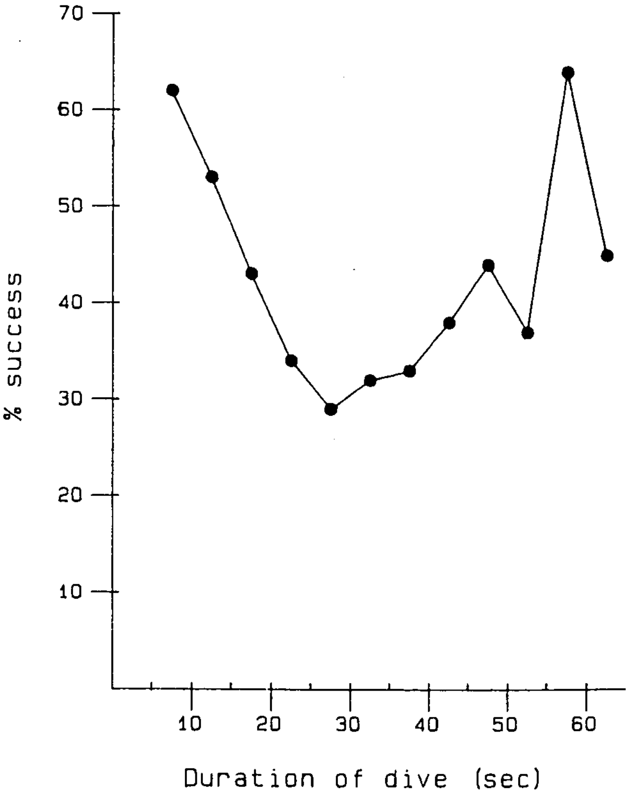

Figure 77 Percentage of dives which were successful after different times under water

in prey handling time when eating and landing a large fish. This aspect is being studied at the moment.

The increase in diving success with depth did not appear to be due to differences in population density of fish, but to the fact that otters spent a longer period fishing along the bottom. However, to complicate matters, it also appeared that success varied with dive length, irrespective of depth (Figure 77). At first, the number of prey caught decreased, the longer an otter spent under water, but, for dives of over 25 seconds, success increased again, suggesting a change in fishing strategy. Also, increase in prey size with depth was not related to differences in population composition of fish; in other words, otters selected differently at greater depths.

A picture is emerging of how otters select and catch their fish, but more observations are needed, especially under water. Radio-collared otters are now being monitored with the aid of diving equipment, and further research on their spatial organization is being undertaken.

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Programme 11
ANIMAL SPECIES INTERACTIONS AND COMMUNITIES

RECOLONIZATION OF HARTLAND MOOR BY SPIDERS

On 14-16 August 1976, a severe fire destroyed 195 ha of heathland at Hartland Moor NNR in Dorset. This area represented about 80% of the dry heath on the Reserve, in addition to a large part of the wet heath and bog, and the destruction of heathland provided an opportunity for a major study of the recolonization of the burnt area by spiders. Previous work on a much smaller burnt area on the same Reserve 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 (Merrett 1976), but that some changes still occur for up to at least 20 years after burning (Merrett 1983). The important features of the 1976 fire were that both the area covered and the intensity of the fire were much greater than in the earlier study, and, perhaps most important of all, that a large part of the burnt area was surrounded by agricultural grassland, 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 any serious long-term effect, but the recolonization by spiders of burnt areas close to unburnt heathland and those close to grassland were thought worth comparing.

Since early October 1976, changes have been studied on 8 plots in the burnt area at Hartland Moor. Six plots are on dry heath, 2 being close to adjacent grassland, 2 in the centre of the burnt area and 2 close to unburnt heathland. The other 2 plots are on wet heath for comparison, one being close to unburnt heath and one close to the grassland. Spiders have been collected by 2 main methods at each plot.

1. To catch ground-active species, a grid of 9 pitfall traps, arranged as 3 rows of 3, 40 m apart in each direction, was used continuously from October 1976 to October 1979. The middle row of traps at each plot was then removed, and the remaining 6 traps used continuously until the present time. The traps used were plastic pots, 8 cm diameter, containing ethylene glycol as a preservative. They were emptied fortnightly at first, when changes occurred rapidly and surface erosion was a problem, but the frequency of emptying was gradually reduced by the third year, after which time 2-monthly emptying appeared to be adequate. As the phenology of spiders on Dorset heathland is already known from earlier work (Merrett 1967, 1968, 1969), the results were summed annually from October to October for each pitfall trap and each plot.

2. To catch aerial migrants, 6 'water traps' located between the pitfalls were used continuously from October 1976 to October 1979. The number of traps was then reduced to 4 at each plot, and they were removed completely in October 1981, when aerial migration appeared to have reached a low level. The traps were plastic trays, 55 cm × 25 cm, supported on a brick above ground level and containing ethylene glycol. Spiders were removed at the same intervals as with the pitfall traps, and the results again summed annually.

Two other collecting methods were used during 1979 and 1980 in an attempt to assess absolute numbers of spiders per unit area. First, on 3 occasions, in May, July and September 1979, 8 quadrats of 0.25 m^2 were searched by hand on each plot between the pitfall traps, and all spiders seen were collected. Second, on 3 occasions, in September 1979 and in June and September 1980, 10 samples of 1 m^2, each comprising 11 sub-samples, were taken in each plot using a D-vac suction net. Because both these methods proved to be relatively unproductive, they were not used in later years.

The percentage cover of each plant species and percentage of bare ground were recorded in one fixed 0.5 m^2 quadrat near each pitfall and water trap during April 1978, September 1979, July 1981 and July 1984.

Numbers of species and individuals

Over the 8 years, a total of 264 species of spiders has been recorded, which represents over 42% of the British spider fauna. Of these, 191 were found in the water traps, which were used between 1976 and 1981, and 215 in the pitfall traps between 1976 and 1984. Thus, 49 species were found exclusively in the water traps and 73 exclusively in the pitfalls. The total numbers of species and adult individuals from all plots taken in the pitfalls in each of the 8 years are shown in Table 29 (the actual totals of individuals caught in 1979-84 have been multiplied by 3/2 to compensate for the reduction in number of traps from 9 to 6 per plot). Also shown is the number of species reaching a peak in numbers in each year. It is clear that, with the exception of the second year, the number of species has increased steadily, as has the number of species reaching maximum numbers in any one year. The high number of species recorded in the second year was probably caused largely by a peak of temporary immigrants which were unable to survive in subsequent years. The total number of individuals is greatly influenced by changes in a few very abundant species, but there has been little overall change since the second year after the fire.

Table 29. Total numbers of species, adult individuals, and species reaching maximum numbers in each year, taken in the pitfall traps at Hartland Moor NNR. Totals of individuals caught in 1979-84 have been multiplied by 3/2 to correct for a reduction in number of traps from 9 to 6 in each plot

Year	Number of species	Number of individuals	Number of species with maximum numbers in year
1976-77	101	3 583	11
1977-78	126	22 384	30
1978-79	111	18 155	15
1979-80	121	20 482	14
1980-81	119	26 920	14
1981-82	138	22 495	25
1982-83	139	23 440	30
1983-84	143	18 114	43

Differences between water traps and pitfall traps

The results obtained from the water traps were interesting in several ways. First, the 49 species which were exclusive to the water traps included a number which are normally never found on open, treeless heathland, eg *Clubiona corticalis, Xysticus lanio, Philodromus praedatus, Achaearanea simulans, Araneus triguttatus*, and *Moebelia penicillata*. These species must have been caught during random migration, and would not have remained on heathland. Second, some heathland species were caught in the water traps in widely different habitats from those which they normally occupy on heathland. For example, *Anelosimus aulicus* and *Araneus cucurbitinus*, which normally live on tall gorse bushes, were found on the recently burnt heathland about 0.5 km from the nearest gorse bushes, and *Pirata tenuitarsis* and *Dolomedes fimbriatus*, usually found on wet heathland and bog, were caught on dry heath on top of a hill. Third, most species were caught in very different numbers in the water traps and pitfalls. As would be expected, many species of web-spinners in the families Theridiidae and Araneidae which are rarely caught in pitfalls were caught frequently in the water traps. Perhaps more surprising was the occurrence of much larger numbers of some adult wandering spiders in the water traps than in the pitfalls during the first few years after the fire (eg *Clubiona trivialis, C. subtilis, Cheiracanthium virescens, Philodromus aureolus, P. cespitum)*. These species would be expected to be found among more mature heather, but it was surprising to find them migrating aerially so frequently on burnt heathland. Conversely, many species which were abundant in the pitfalls were found rarely in the water traps, even including some early colonists of burnt heathland, which might be expected to migrate aerially (eg *Haplodrassus dalmatensis, Arctosa perita, Steatoda albomaculata, Phaulothrix hardyi*). It was notable that, although abundant in the pitfalls, not a single specimen (either adult or juvenile) of the genera *Zelotes, Gnaphosa or Agroeca*, and only 2 juveniles of *Alopecosa* were caught in the water traps. It would seem, therefore, that these genera recolonize burnt heathland mainly, if not entirely, by walking, rather than by aerial immigration. As expected, species which were about equally common in both the pitfalls and water traps during the first few years included linyphiids which are well known as common aeronauts and colonizers of newly created habitats, eg *Oedothorax* spp., *Erigone* spp., *Pelecopsis parallela, Milleriana inerrans, Savignya frontata, Porrhomma microphthalmum, Meioneta rurestris, Bathyphantes gracilis, Lepthyphantes tenuis.*

Effects of surrounding grassland

During the first 2-3 years after fire, several species typical of grassland habitats were caught in considerable numbers, but these declined rapidly in later years, as the heather grew up. At first, there was some evidence that these species occurred mostly in the plots nearest to the grassland, but, probably because of their efficient dispersal, they spread rapidly to the other plots. Conversely, there was also a tendency for some of the heathland species which apparently do not migrate aerially to appear and reach high numbers first in the plots nearest to the unburnt heathland, but this effect was also only transitory. Overall, it seemed that the fact that about 70% of the burnt area was surrounded by grassland had little or no effect on the spider populations present beyond the third year after burning.

Changes recorded by pitfall trapping

The results derived from the pitfall trapping programme form the most important part of this work, partly because the pitfalls have been used throughout the whole duration of the project, and partly because they are the most effective method of catching most of the

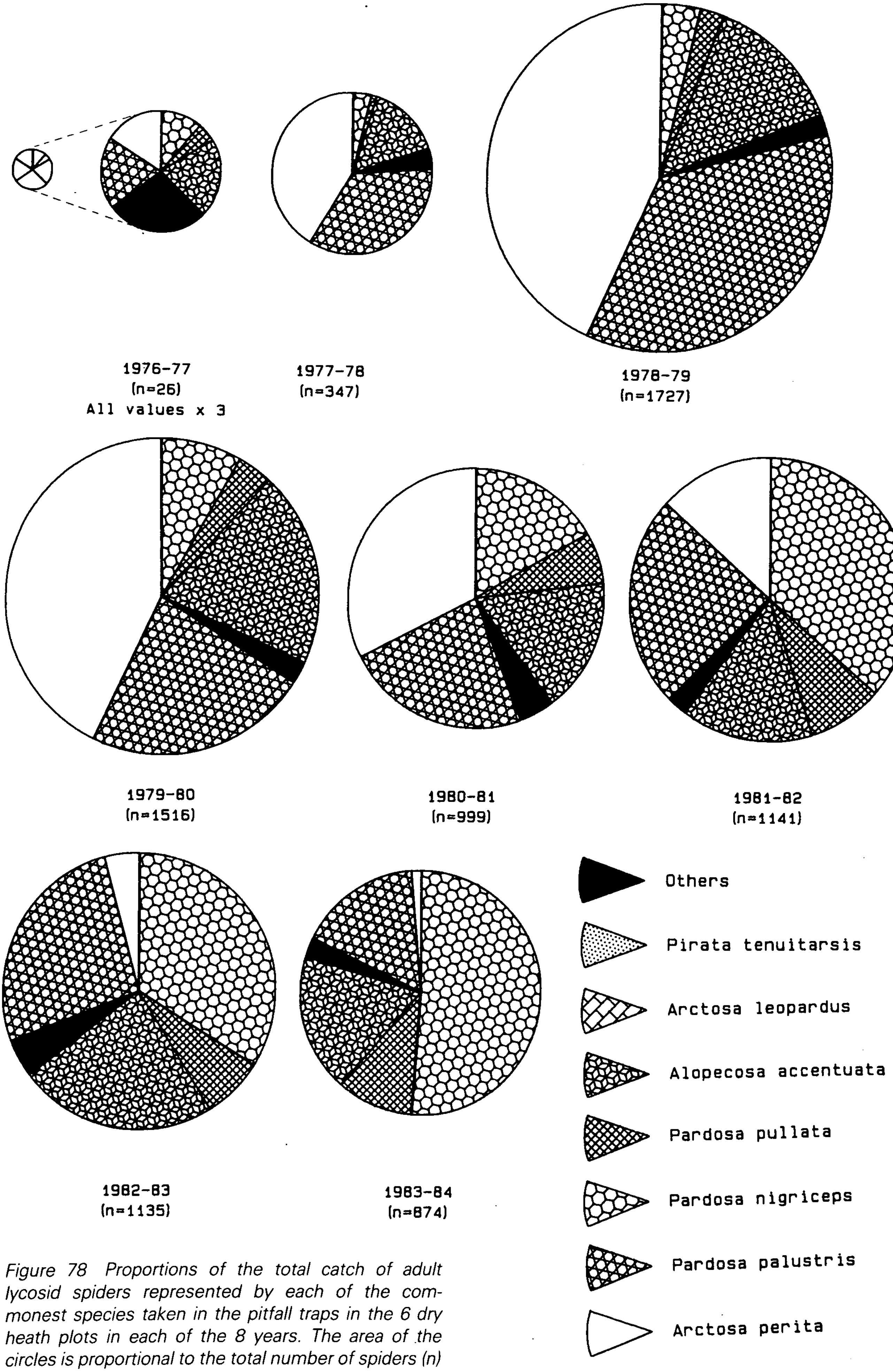

Figure 78 *Proportions of the total catch of adult lycosid spiders represented by each of the commonest species taken in the pitfall traps in the 6 dry heath plots in each of the 8 years. The area of the circles is proportional to the total number of spiders (n)*

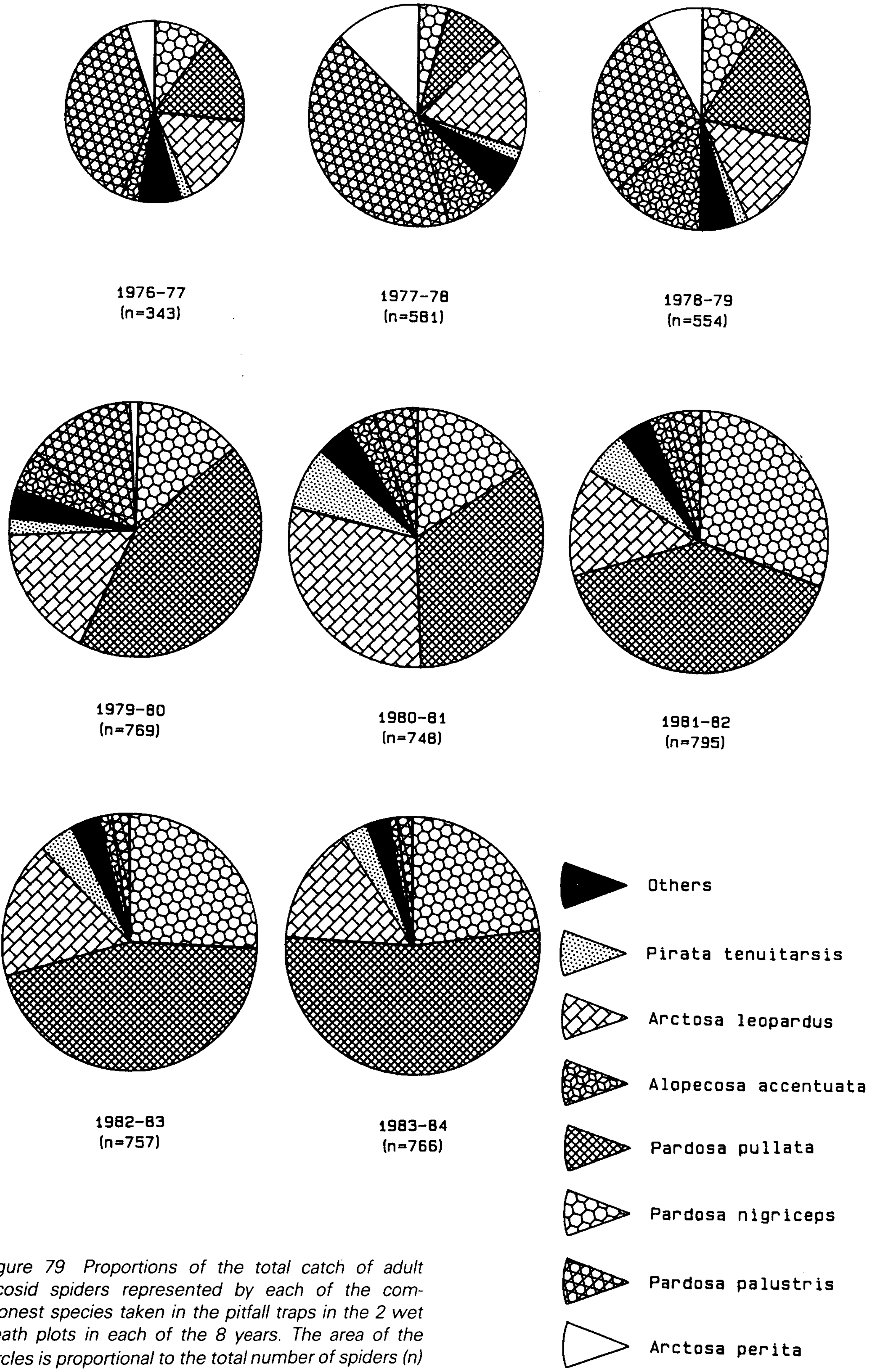

Figure 79 Proportions of the total catch of adult lycosid spiders represented by each of the commonest species taken in the pitfall traps in the 2 wet heath plots in each of the 8 years. The area of the circles is proportional to the total number of spiders (n)

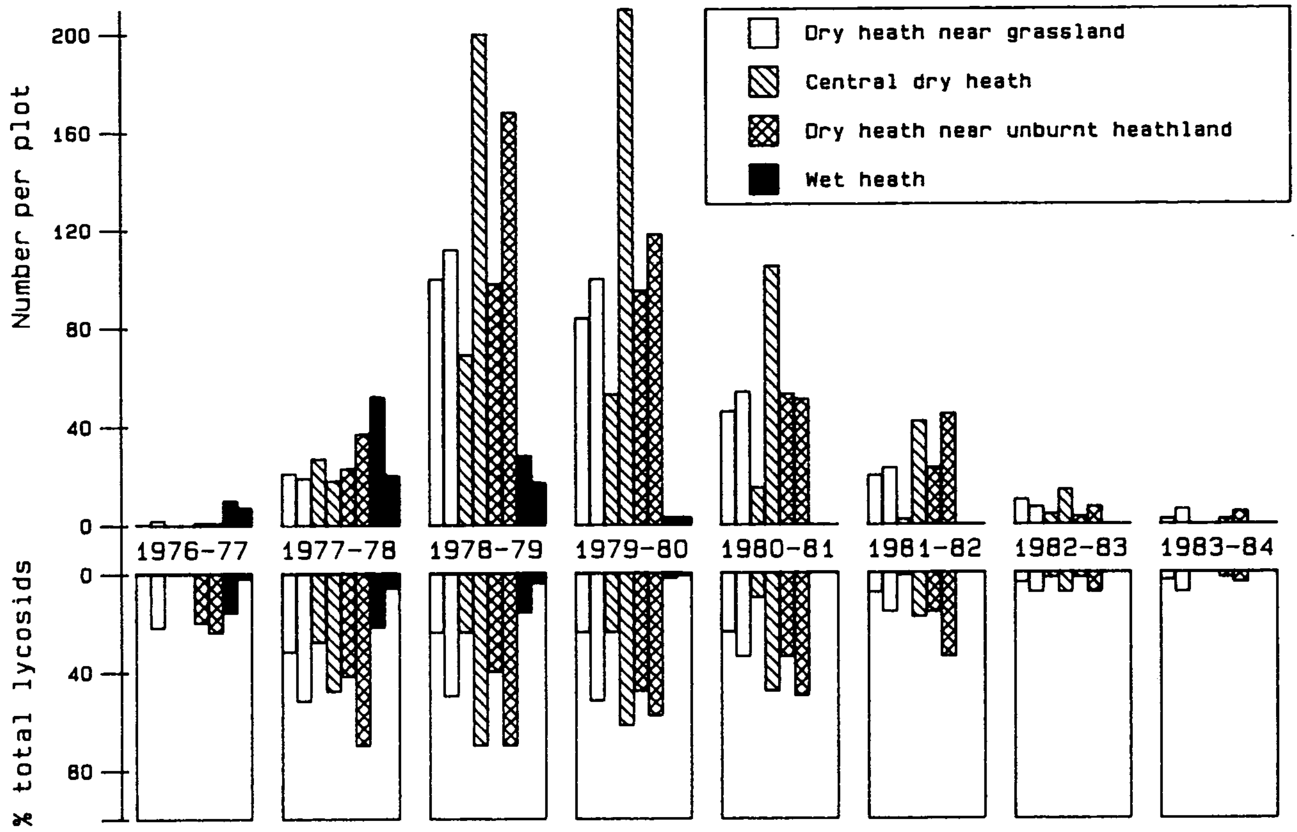

Figure 80 Number of adults of Arctosa perita *taken in pitfall traps in each plot in each year (above), and expressed as a percentage of all adult lycosids in each plot (below). Numbers for 1979-84 multiplied by 3/2 to correct for reduction in numbers of traps from 9 to 6*

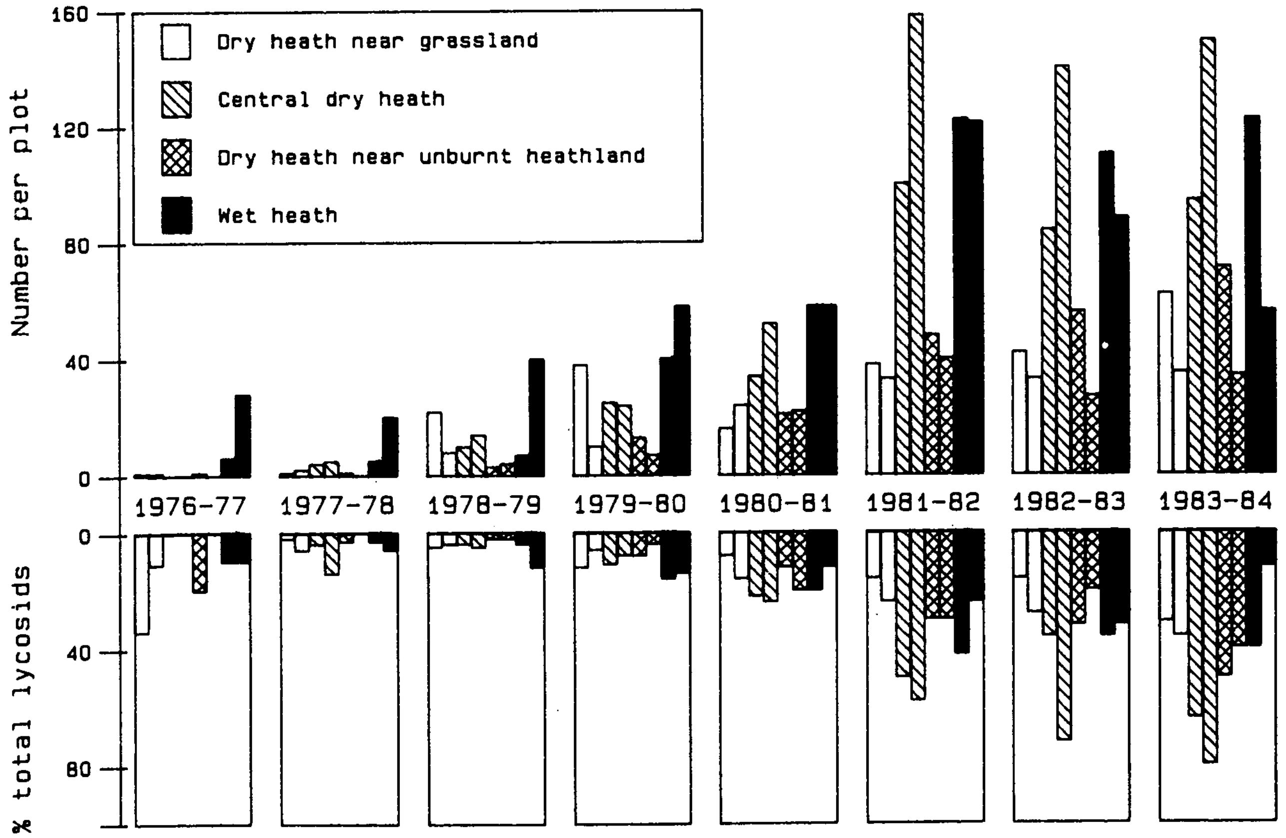

Figure 81 Numbers of adults of Pardosa nigriceps *taken in pitfall traps in each plot in each year (above), and expressed as a percentage of all adult lycosids in each plot (below). Details of plots as in Figure 80*

spider species on heathland. It is not possible in this brief account to do more than describe a few small samples of these results, but the wolf spiders (family Lycosidae) provide a good range of examples of the trends shown by other families. Taking the total catches of adult wolf spiders for each year from the 6 dry heath plots and the 2 wet heath plots separately, Figures 78 and 79 show the proportions of the total lycosid fauna represented by each of the commonest species.

In the dry heath plots (Figure 78), *Arctosa perita*, a species which lives on coastal sand dunes and other open, dry, sandy habitats inland, formed the largest proportion of the total in the second to fourth years after burning, and subsequently declined so that it had almost disappeared by 1984. *Pardosa palustris*, a typical species of heathland with some bare areas, also declined after the third year, but less markedly so. The decline in these 2 species was matched by a corresponding increase in the numbers of *Pardosa pullata* and *P. nigriceps*, especially of the latter from the fifth year onwards. *P. nigriceps* is more arboreal than the other lycosids, and therefore its population increases as the heather grows up. *P. pullata* is found mainly in wetter habitats, and is only present in reasonable numbers on dry heath when the heather becomes mature and provides a more humid microclimate. The fifth common species, *Alopecosa accentuata*, showed no change in relative abundance throughout the 8 years. A further 10 species which occurred in small numbers at one time or another comprised the category 'others'.

When the results for the wet heath plots (Figure 79) are compared with Figure 78, the most obvious difference is that the total numbers caught varied much less in the wet plots from year to year. Because the fire was less severe in its effects on the wet heath, the vegetation recovered much more quickly. In later years, variations caused by summer drought or temperature changes are also less likely to be evident in the wet heath. Comparing the individual species, *A. perita* was always much less common in the wet plots, and had disappeared by the end of the fourth year. *P. palustris* was as abundant as in the dry plots during the first 4 years, but also declined greatly thereafter. *P. nigriceps*, and especially *P. pullata*, however, increased more rapidly than in the dry plots, the latter becoming clearly the dominant species after the sixth year. Two typical wet heath and bog species, *Arctosa leopardus* and *Pirata tenuitarsis*, were found on the wet plots, but not on the dry plots. They did not, however, show any consistent changes in relative abundance during the 8 years. *A. accentuata* remained relatively infrequent. The category 'others' in the wet plots comprised 11 species, 3 of which were not taken in the dry plots.

The details of the pitfall trap catches of *A. perita* and *P. nigriceps* from separate plots are given in Figures 80 and 81. The histograms for *A. perita* (Figure 80) show clearly the early peak in the wet plots in 1977-78, followed by its rapid disappearance, whereas in the dry plots the peak in numbers was not reached until 1978-79 and the species persisted for much longer afterwards. The lower totals shown in dry heath plots 3 and 5, in comparison with plots 4 and 6, are probably related to the fact that plots 3 and 5 were damper, as indicated by the larger amounts of purple moor-grass (*Molinia caerulea*) in these plots. In the earlier study (Merrett 1976), *A. perita* reached its maximum numbers in the second year after the fire, probably because it was able to colonize the much smaller burnt area more quickly.

Similarly, the results for *P. nigriceps* (Figure 81) show, at first, a more rapid increase in numbers in the wet plots, but in this species there has been no noticeable subsequent decline in the wet plots in comparison with the dry plots, and numbers have remained roughly constant from the sixth year onwards.

A remarkable feature of both Figures 80 and 81 is the consistency in shape of the histograms from year to year.

It is hoped to continue the pitfall trapping alone until about 15 years after the fire, by which time changes in the spider population will probably have become greatly reduced.

P Merrett

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PHYTOPHAGOUS INSECTS ON ISOLATED COLONIES OF HOST PLANT: COLONIZATION, PERSISTENCE AND INTRODUCTION OF SPECIES

There is increasing need to know the minimum areas of habitat which will support viable populations of wildlife. One approach to this question has been to monitor the persistence of phytophagous insects on well-defined stands of host plant. By the suitable choice of a plant species, it is possible to define its distribution and local abundance quite accurately, and to observe the distribution and survival of dependent insects.

This account describes a study on dyer's greenweed (*Genista tinctoria*) using 5 out of 9 known sites in the Stamford area and one of 3 in the Huntingdon area. A similar, larger study has been carried out on common rock-rose (*Helianthemum chamaecistus*). The first objective was simply to record the presence and persistence of 5 species of host-restricted insects (Table 30) at the 6 sites between 1980 and 1984, and any gains or losses through colonization or extinction. The second objective was to introduce certain species to sites where they were absent; success or failure in establishment would help to show whether dispersal or other factors were important for the observed occurrences of species. Other possible host plants may occur in gardens, but are unlikely to provide significant additions for the survival and dispersal of dependent insects.

Site visits were made at about weekly intervals during June, when the insects could be observed most readily, either as adults or larvae. The presence of leaf miners and galls was determined by visual searching. The leaf miners had a short period of larval life when they could be found. The optimum period varied from year to year so the timing of searches could be critical, especially when population levels were low. The free-living species could often also be recorded visually, but suction samples were usually taken for this purpose. Failure to record any species at a site by missing the appropriate sampling period was termed 'no data'. Four of the stands were very small and compact and could be intensively searched, or sampled. The *G. tinctoria* at Collyweston was very extensive and only a small portion was ever examined.

Introductions were made at 3 sites, where a species was deemed to be absent after nil records for 2 or more successive years. In the case of the 2 Hemiptera, adults were collected and liberated on the same day. Adults of the moth *Leucoptera wailesella* were reared from mines and liberated in batches, within 2-3 days of emergence. The leaf-mining and gall-forming Diptera were not successfully reared, or introduced.

The results of this study provide a 6 site × 5 species × 5 year matrix with 150 elements (Table 31). Of these, 53 were represented by pre-existing colonies, while 8 were artificially established colonies. There were 76 nil records, and only one case (out of a possible 33) when natural colonization was thought possibly to have taken place during the course of the study, ie a positive record after 2 successive nil records and no introduction. This record was for the mirid *Heterocordylus genistae* at the Stamford site in 1982. It was much the most widespread species

Table 30. Principal features of 5 insect species feeding on *Genista tinctoria*

Code	Species	Order, family	Stage(s)	Period
A	*Agromyza pulla* Meigen	Diptera, Agromyzidae	Larva-mine	18·6-1·7
J	*Jaapiella genisticola* (Löw, F)	Diptera, Cecidomyiidae	Larva-gall	8·6-5·7
H	*Heterocordylus genistae* (Scopoli)	Heteroptera, Miridae	(Larva), adult	(5·6) 18·6-31·7
U	*Livilla ulicis* (Curtis)	Homoptera, Psyllidae	Adult	5·6-6·7
W	*Leucoptera wailesella* (Stainton)	Lepidoptera, Lyonetiidae	Larva-mine	18·6-1·7

Table 31. Size and isolation of 6 *Genista tinctoria* stands with the occurrence of 5 insect species 1980-84

	Size (m^2)	Nearest neighbour (km)	1980	1981	1982	1983	1984
Collyweston	>100	35	A J H U –	A J H U W	A J H U W	A J H U W	A J H U W
Stamford	8-16	4·5	. . . . –	. . . (U) .	. . H . (W)	. . H (U) **W**	. . H . **W**
Lincs Gate	2-4	1·5	†– . H U –	– . H – .	A . H U .	. . H . .	A . H . .
Ketton	1-2	3·5	. . H . –	. . H (U) .	. . H **U** .	. – – **U** .	. . H **U** .
Ufford	1-2	10·5	. J †– U –	. J H U .	. J H U .	. J H U .	. J H U .
Woolley	2-4	6·0	. . . . –	. . (H) (U) .	. . **H** . .	. . **H** (U) .	. . **H** . .
Total number of sites per species			1 2 3 3 –	1 2 4 2 1	2 2 6 4 1	1 2 5 3 2	2 1 6 3 2

† Species recorded here in 1978
. Nil record
— No data
A Species present

(A) Species introduced
A Species established from introduction
Code letters as in Table 30

found on *Genista* (9 of the 12 sites originally mentioned), and was successfully established at Woolley after the introduction of 20 adults and 30 larvae on 1-3 July 1981.

The psyllid *Livilla ulicis* was successfully introduced at Ketton (40 adults), but not at Stamford or Woolley, despite 2 attempts with 25 and 50 individuals in each case. It occurred in large numbers every year at the small remote Ufford site, but was less regularly recorded at the Lincolnshire Gate site, where the plant population was severely reduced by herbicide drift from the adjoining field in 1983.

The leaf-mining agromyzid fly was likewise irregularly recorded at Lincolnshire Gate. Elsewhere, it was only seen at the very large Collyweston site, where all 5 species occurred. The gall midge *Jaapiella genisticola* and the moth *Leucoptera wailesella* were also very restricted in distribution, though the latter was successfully established at Stamford from 15 males and 18 females introduced between 5 and 14 July 1982.

Genista tinctoria has probably always had a very scattered distribution in this area, with small persistent populations at many of the sites. The Stamford population appeared to be a relatively recent one, as it was still spreading on sparsely vegetated spoil from a quarry and had few species of phytophagous insects for its size.

The insect species studied must be those that are highly adapted to persistence at low densities and to occasional long distance dispersal to colonize new sites. Successful introduction of 3 species at 3 sites suggests that introductions could greatly supplement natural colonization. Failure at 2 sites, however, shows that timing and/or local conditions may be critical. All colonies on very small isolated sites are continuously vulnerable to chance extinction from external factors. The Ketton site was itself totally destroyed in September 1984.

B N K Davis

WHY DO SOME INSECT SOCIETIES HAVE SO MANY QUEENS?

The honeybee (*Apis mellifera*) conforms to the popular image of an insect society. Most laymen know that bees have a single large queen, who lays all the eggs, and that these are tended by a work force of sterile females called 'workers'. A young queen is reared in early summer and, after mating with drones from other colonies, she returns to the hive. She usually takes control of the colony, forcing the old queen to leave. The old queen takes a retinue of workers with her, and so the colony divides or 'swarms'. The common wasp (*Vespula vulgaris*) similarly has a single large queen that controls a worker force, but the colony has an annual life cycle and dies at the onset of winter. Only young fertile queens hibernate and survive to found new colonies in the next year. A wasp colony spends most of the season building up a worker force during a sort of 'vegetative growth' or 'founding phase'. It reaches maturity and 'seeds' at the end of the season, when it produces large numbers of young queens and males. The colony is forced to have an annual life cycle because it cannot control its next environment in the way bees can. The dangers associated with hibernation and colony foundation cause the excessive sexual production, compared with bees which have a very high probability of one half of their colony surviving. In some warmer parts of the world, wasps have been able to establish perennial colonies.

Ant colonies have a similar social structure to a perennial wasp colony. All ants have evolved a perennial habit, because they usually nest in the soil, which is well buffered against the extremes of climate. Termites, or white ants (Isoptera), are not ants at all, but belong to quite a different order of insects, more closely related to the cockroaches. Consequently, their social system has a different genetic basis to the 3 hymenopteran social insects discussed here. The main difference is that both male and female termites have equal roles in the life of the colony.

Although a single queen (monogyny) is considered to be usual in all 4 of these groups of truly social insects, it is possible to find species that normally have more than one queen in a colony (polygyny). Much of the theory of the evolution of social systems of insects is based upon the idea that all the members of a colony are closely related - usually a mother and her daughters. Colonies which have several queens that may not be closely related have a lower average relatedness among their workers than monogynous colonies, and are difficult to accommodate within the theory (eg Pearson 1982). One explanation is that polygyny is an adaptation that enables a founding colony to spread by swarming, and so monopolize isolated habitats - in effect becoming a 'super-colony'. Another explanation is that the queens accrue some mutual advantage by reciprocal co-operation.

Polygynous species were found fairly regularly in the ants and wasps, but only recently has it been realized that a high proportion of ant species are polygynous. The big colonies of many monogynous species are very obvious, while polygynous species are less obvious, though there may be more species and more colonies in this group. Work by ITE has shown that all *Myrmica* species are polygynous, although only a few years ago it was thought that only a few species, such as *M. rubra*, had many queens. Current interest in the problem of explaining the evolution of polygyny has made this area of research very popular. Since the

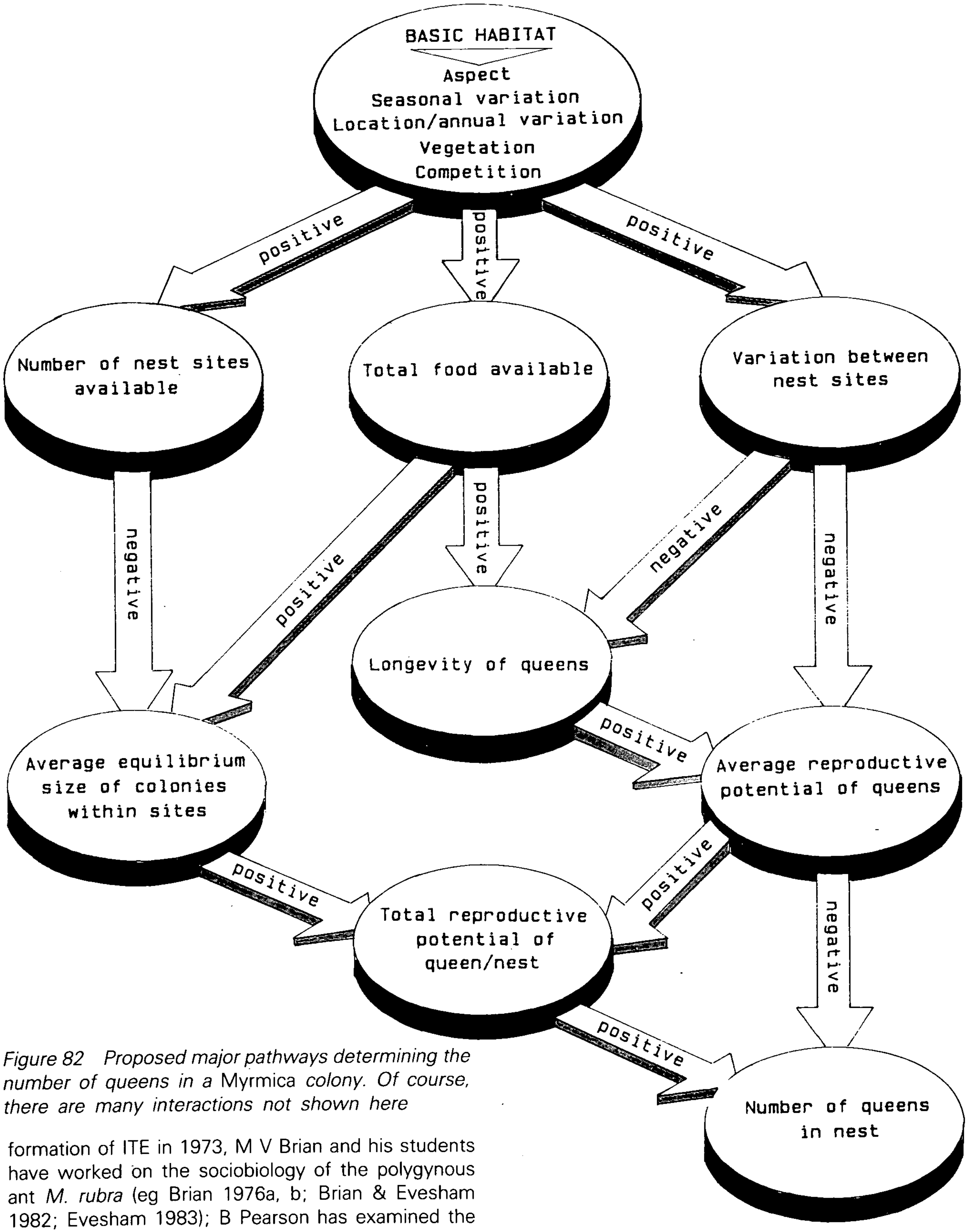

Figure 82 Proposed major pathways determining the number of queens in a Myrmica *colony. Of course, there are many interactions not shown here*

formation of ITE in 1973, M V Brian and his students have worked on the sociobiology of the polygynous ant *M. rubra* (eg Brian 1976a, b; Brian & Evesham 1982; Evesham 1983); B Pearson has examined the genetic structure of *M. rubra* colonies (eg Pearson 1977, 1982); and G W Elmes has compared the population ecology, physiology and morphology of most of the British species of *Myrmica* (eg Elmes 1975, 1976; Elmes *et al.* 1980; Elmes & Wardlaw 1983). Nests of all the *Myrmica* ant species have been shown to recruit new queens. There is genetic evidence that the queens within individual nests of *M. rubra* are not closely related, and there is circumstantial evidence that the same is true for other *Myrmica* species; queen turnover is high, implying a short life for queens in natural colonies. High queen mortality helps to explain the high natural variability of queen members, and indeed the existence of some queenless colonies. There is no evidence for the existence of super-colonies of *Myrmica*, as most species occupy a habitat in competition with other ants. The second explanation for polygyny, that queen mortality provides a reason for co-operation among queens, seems more likely. Ant colonies reproduce more slowly than those of wasps or bees, so that the founding phase can last a considerable number of years. If environmental factors lead to a high mortality of queens, then colony foundation may be a poor option for a young queen, compared to joining and co-operating with an existing colony. Established colonies therefore fluctuate about the mature state, entering a temporary growth phase if environmental change permits. A possible system of control is summarized in Figure 82.

The 'quality', or reproductive effectiveness, of queen ants varies with age and size. Large queens are generally more productive than small ones. For any nest, the total effective queen level is the sum of the individual 'qualities', which makes detailed analysis complicated, because the 'quality' of queens may vary between nests, within a habitat, and between habitats. There is a considerable variation in size between the queens of the various *Myrmica* species and, as a rule, the largest queens are the most productive and least polygynous. So, provided that data on queen turnover and 'quality' can be collected for a few more species, a single set of equations can be formulated to predict the population structure of *Myrmica* ants at the colony, habitat and species levels. Such equations will have an immediate practical use in understanding the social factors which affect the survival of larvae of the rare large blue butterfly (*Maculinia arion*) in the nests of their host *Myrmica* species (Thomas 1980, 1983).

G W Elmes

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IMMUNOLOGICAL CROSS-REACTION BETWEEN TRYPANOSOMES OF BATS AND MAN

Trypanosomes of the subgenus *Schizotrypanum* are common parasites of bats (Chiroptera) in this country and elsewhere. This subgenus also contains an important pathogen of human beings in South and Central America, *Trypanosoma cruzi*. The species found in British bats, while not infective to man, resemble *T. cruzi* in many ways and can serve in some respects as laboratory models for the latter. The object of this study was to determine whether the 2 British species, *T. dionisii* and *T. vespertilionis*, had antigens which would cross-react with antibodies developed against *T. cruzi*.

Antigens were prepared from *T. dionisii* (CCAP 1981/1) and *T. vespertilionis* (CCAP 1981/10), grown *in vitro*, by freeze-thawing and sonication. A freeze-thawed preparation of *T. cruzi* strain Y was provided by Dr D Snary

Table 32. Log reciprocal end-point titres of titrations of 4 trypanosomal antigens against mouse and human anti-*T. cruzi* sera by ELISA (end-points taken as highest dilution with mean optical density - SE greater than twice the mean optical density + SE of cells without antigen)

Experiment number	Sera	Antigens			
		T cruzi X10	*T cruzi* Y	*T. vespertilionis*	*T. dionisii*
1	Mouse	4	3	3	3
	Human	4	4	4	4
2	Mouse	3	3	3	3
	Human	3	3	3	3
3	Mouse	3.3	3.3	3.0	3.0
	Human	3.6	3.6	3.6	3.3
4	Mouse	3.3	3.3	3.0	3.0
	Human	3.6	3.6	3.3	3.3

Experiments 1 and 2: 10-fold dilutions of sera; based on means of 3 experimental determinations in experiment, 1, 1-3 in experiment 2
Experiments 3 and 4: doubling of antigens; based on means of determinations

(Wellcome Research Laboratories) and soluble antigens from *T. cruzi* strain X10, extracted by boiling sodium dodecyl sulphate followed by Triton X-100, were provided by Dr M J Turner (MRC Biochemical Parasitology Unit).

These antigens were tested against pooled antisera from human patients and mice infected with *T. cruzi* (supplied by Dr M A Miles, London School of Hygiene and Tropical Medicine), by the enzyme-linked immunosorbent assay (ELISA); optical density (OD) was read in a 'Plateskan' apparatus.

The results, summarized in Table 32, indicate considerable cross-reactivity between *T. dionisii* and *T. vespertilionis* antigens and *T. cruzi* antisera. Although higher ODs were usually given by the *T. cruzi* X10 antigen when titrated against serum dilutions in experiment 1, and by both *T. cruzi* antigens in experiment 2 (in which activity was markedly reduced), end-point titres were the same for all antigens, except for *T. cruzi* X10 in experiment 1. When antigen dilutions were titrated (Table 32), the 2 *T. cruzi* antigens gave end-points one dilution higher than the other 2 antigens (note, however, that these were only doubling dilutions). The conclusion, therefore, is that *T. dionisii* or *T. vespertilionis* antigens would be as effective as the *T. cruzi* antigen in detecting *T. cruzi* antisera by ELISA.

Acknowledgements
ITE thanks Drs Snary, Turner and Miles for gifts of antigens and antisera.

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A MALARIAL PARASITE OF BATS

As part of a study of the protozoan blood parasites of British bats, blood films were collected during 1983-84 from over 350 bats representing 9 of the 15 British species. The malarial parasite, *Polychromophilus murinus* (Dionisi 1899), was found in the blood of Daubenton's bats (*Myotis daubentoni* Kuhl 1819). This parasite was first described from the blood of Italian bats (Dionisi 1899), and has since been recorded from bats of various parts of the Old World.

Species of the genus *Plasmodium*, which cause malaria of man, multiply within erythrocytes and destroy these in large numbers, causing anaemia and the characteristic periodic fevers. Unlike these species, however, *P. murinus* multiplies in lymphoid tissue cells, and only gamete-producing cells - gametocytes - develop in the host's erythrocytes; it is not therefore obviously harmful to the bat. Wingless flies (Diptera, Nycteribiidae), obligate blood-sucking ectoparasites of bats, have been suspected of transmitting *P. murinus* in other parts of the Old World, though the actual vector species has only rarely been definitely determined (Garnham 1977). The gametocytes are ingested by the nycteribiid in its bloodmeal; gametes are produced in the fly's gut and fertilization takes place; the resulting zygote penetrates the gut wall to form an oocyst on its outer epithelium. The parasite multiplies asexually in the oocyst to produce a large number of sporozoites which eventually migrate to the nycteribiid's salivary glands, from where they are injected with the insect's saliva into the next bat on which it feeds. Three species of Nycteribiidae have been formerly recorded from British bats, but in recent years only *Nycteribia kolenatii* Theodor & Moscona 1954 has been reported frequently; apart from a single specimen on a Natterer's bat (*M. nattereri*), *N. kolenatii* has been found only on *M. daubentoni* (Hutson 1984).

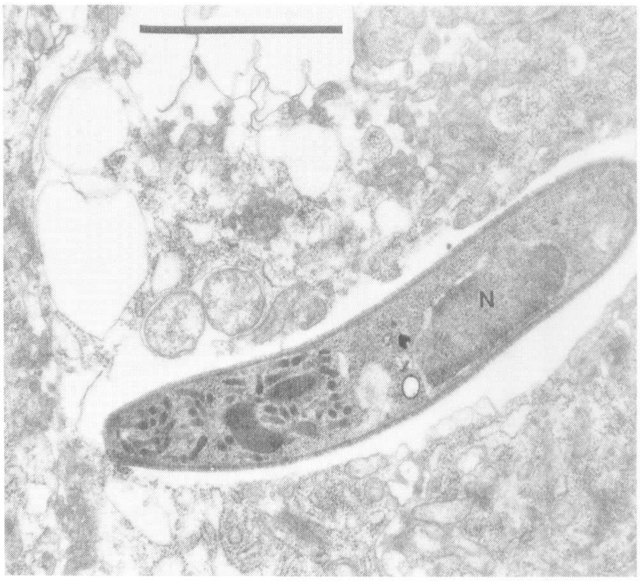

Plate 32 Transmission electron micrograph of thin section through a sporozoite of Polychromophilus murinus *in salivary gland of* Nycteribia kolenatii
N = sporozoite nucleus: scale bar = 1 μm
(Photograph R A Gardner)

Gametocytes of *P. murinus* were found in the blood of 29 out of 115 *M. daubentoni* examined: 14 of 70 from hibernation sites in East Anglia, 11 of 36 from a summer roost in Northamptonshire, and 4 of 9 from a summer roost in Norfolk. These bats were heavily infested with *N. kolenatii*: of 45 hibernating bats exhaustively searched, 42 were carrying flies, with an average of 4.4 flies per infested bat (range 1-9). *N. kolenatii* were collected, dissected and examined for stages of *P. murinus*. No oocysts were seen on the gut walls of 230 *N. kolenatii* dissected; sporozoites were, however, found in the salivary glands of 6 out of 54 of these flies.

To increase the likelihood of finding parasite stages in the flies, 2 *M. daubentoni* with high levels of gametocytes in the blood were maintained in captivity. Flies collected from other bats were allowed to feed on the

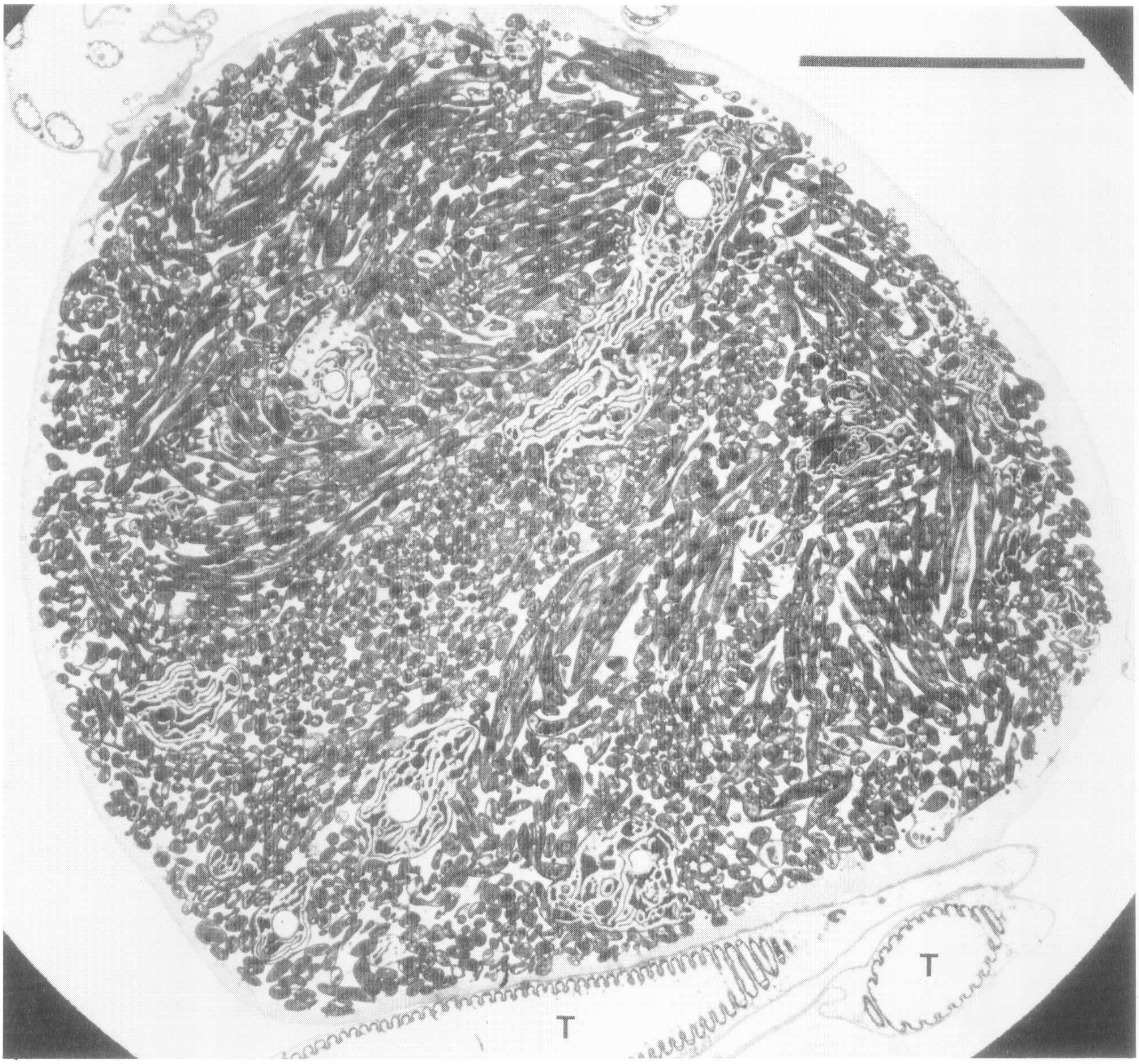

Plate 33 Transmission electron micrograph of thin section through an oocyst of Polychromophilus murinus *on the mid-gut of* Nycteribia kolenatii
T = insect's tracheoles; scale bar = 10 μm
(Photograph R A Gardner)

captive bats for 2 or more weeks and then dissected. Developing and mature oocysts were found in 7 of the 26 flies dissected. Gametocytes in the blood of these 2 bats, sporozoites in the salivary glands, and oocysts on the mid-guts of *N. kolenatii* have been examined by transmission electron microscopy. The ultrastructure of these stages, not previously described, will be compared with that of corresponding stages of other malarial parasites (Plates 32 and 33).

R A Gardner

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Programme 12
CYCLING OF NUTRIENTS

WHERE DO THE SOLUTES IN UPLAND STREAMS COME FROM?

Although streamwater is fundamentally derived from precipitation (rainfall, snow and hail), its chemistry differs markedly (Figure 83). Concentrations of solutes present in precipitation (rain is not pure water) are smaller than those in streamwater: some solutes, absent from precipitation, occur in streamwater. What causes these differences in composition? Most of the water in streams drains from land - very little precipitation falls directly into streams. Before entering a stream, precipitation is likely to be modified as it courses its way through the vegetation canopy, soil and possibly bedrock - the various compartments of an ecosystem. Members of ITE have been sampling water from the different compartments of a small stream catchment in mid-Wales, dominated by 2 main plant communities: a mat-grass (*Nardus*) - bent (*Agrostis*) - fescue (*Festuca*) grassland and a cotton-grass (*Eriophorum*) bog community.

Water dripping from vegetation in the *Nardus* grassland was found to have significantly larger concentrations of most solutes than precipitation, but its acidity was less, a pH of 4·7 compared with 4·4 (Figure 83). Silica, absent from precipitation, was present in measurable concentrations in the vegetation throughfall. These changes can be attributable to 4 main processes:

1. the solution of particles and gas molecules previously deposited on leaf surfaces from the atmosphere during dry weather (these deposits are usually designated 'dry deposition');
2. the leaching and solution of elements from within leaves, a process of 'canopy leaching' that may be accentuated by the acidic nature of precipitation;
3. the uptake of ions from solutions by leaves and/or phylloplane (leaf surface) microbes;
4. the evaporation of water from the leaf surfaces by sensible heat (which produces a concentration effect).

Dry deposition, canopy leaching and evaporation will tend to increase solute concentrations - evaporation by about 12% - while absorption by leaves and leaf microbes will tend to decrease solute concentrations. The increased concentrations of sodium, magnesium, chloride and sulphate are thought to be mainly attributable to the solution of dry deposits of atmospheric origin; potassium and silica are mainly derived from plants, while the sources of the additional calcium and magnesium are varied. Collections of water dripping from *Eriophorum*-dominated vegetation have not yet been fully analysed. While there seem to be increased concentrations of many solutes, the acidity of '*Eriophorum* throughfall', unlike that from the *Nardus* community, is not decreased.

Water dripping from the vegetation canopy generally forms the input to the next compartment, soil, in the ecosystem sequence, but, on rare occasions, it flows across the ground surface, 'surface flow'. The chemistry of the latter is understandably linked closely to that of throughfall.

Water-soil interactions

Vegetation throughfall is modified when it reaches soil by its interplay with soil and its complement of plant roots. It will be influenced by cation exchange, anion adsorption and the solution of organic compounds and soil minerals. The experimental catchments are dominated by 2 soil types - stagnopodzols and peats. The former usually occur beneath the *Nardus* grassland communities, while the peats are found below *Eriophorum* communities. The chemical composition of waters draining from these 2 types of soil differs appreciably. Concentrations of most solutes are smaller in soil waters than in the throughfall from vegetation (Figure 83). Peat drainage and the water in the surface layer (horizon) of the stagnopodzol are nonetheless more acid than throughfall, the increased acidity being partly attributable to the solution of organic acids. Uptake by plant roots and soil microbes, together with the exchange of cations between soil solutions and the surfaces of soil particles, accounts for the decreased concentrations of sodium, potassium, calcium and magnesium and will also contribute to the greater acidity.

Waters from the lower horizons of the stagnopodzol contain augmented concentrations of silica and significant amounts of aluminium, both derived from soil minerals, and probably the secondary products of weathered alumino-silicate minerals.

Water moving vertically downwards through a stagnopodzol profile would be expected to gain considerable amounts of dissolved organic carbon from the organic horizon, while the concentrations of most other solutes would be decreased. On reaching the mineral horizons, it would acquire more silica and aluminium, but would lose some of the organic carbon. On the other hand, the composition of water draining laterally from stagnopodzols to streams, as 'throughflow' or interflow', would depend upon the layer or horizon being traversed, with a marked contrast between water from organic surface horizons and lower mineral horizons. Additionally, the composition of waters draining from stagnopodzols is likely to be influenced by the period of contact between water and soil - the 'residence' or 'contact' time.

Water held by, or moving through, fine soil pores may equilibrate with the soil itself, but water moving rapidly through large soil pores or cavities may never reach equilibrium with the soil matrix. The natural cavities, soil pipes (Gillman & Newson 1980), in the upper mineral (Eag) horizon of the stagnopodzols within the catchment are 5-10 cm in diameter. During very wet conditions, water flows through them rapidly, emerging much more acid, pH 3·93, than the water draining more slowly from the Eag horizon (pH 6·31) (Table 33).

Changes in the composition of throughfall as it moves through *'Eriophorum* vegetation' and its underlying peat formations are broadly similar to those noted for the organic horizon of stagnopodzol. Concentrations of most solutes in 'peatwater' are smaller than in

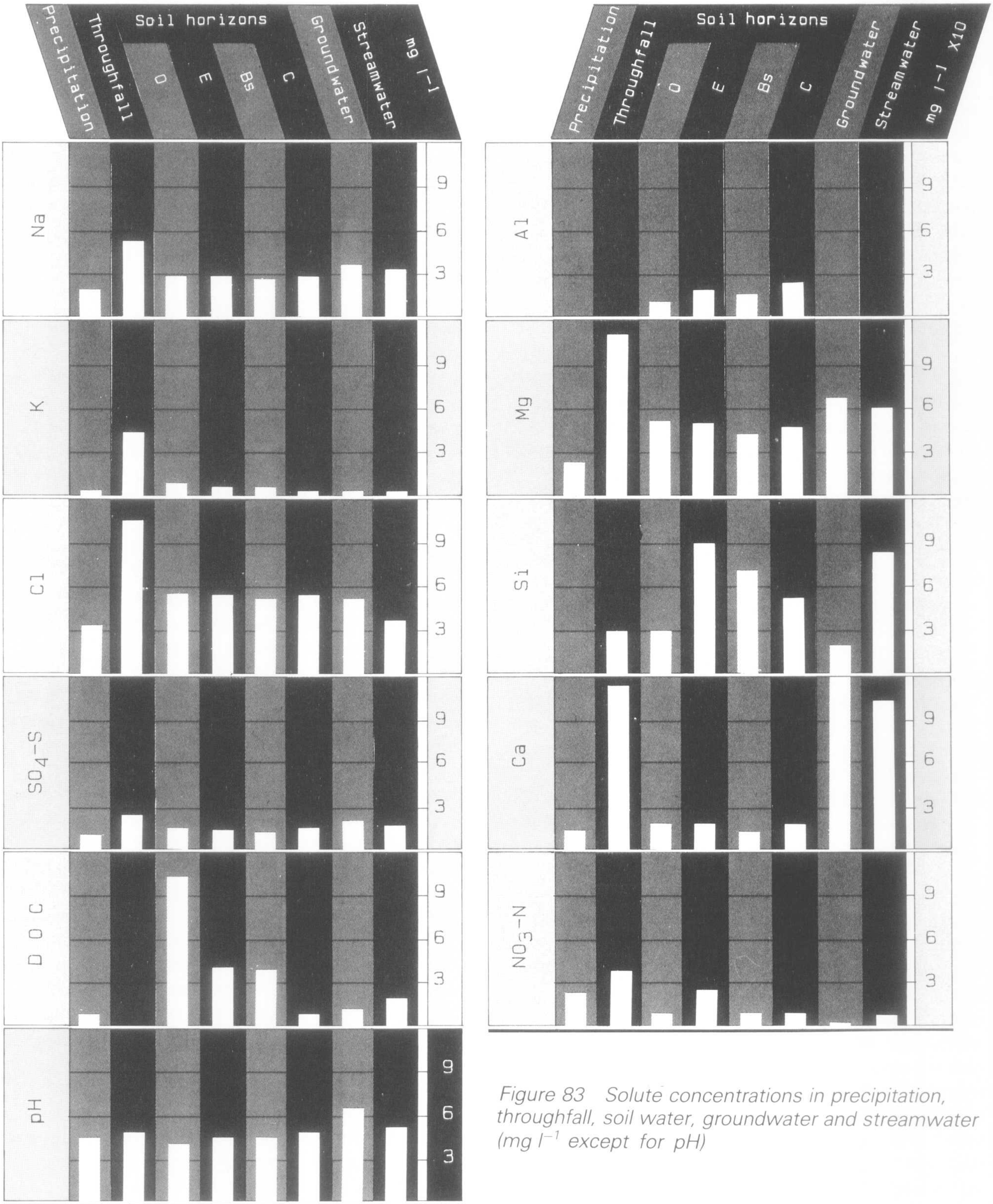

Figure 83 Solute concentrations in precipitation, throughfall, soil water, groundwater and streamwater (mg l^{-1} except for pH)

throughfall, the exception being organic carbon (Table 33). On balance, 'peatwater' is more acid than incident precipitation.

Water-rock interactions

Water draining from soil will penetrate the underlying bedrock as it joins the groundwater reservoir. Most rock-forming minerals react very slowly with percolating water, but, because carbonate minerals are much more soluble than those of alumino-silicate, they can, if present, have a pronounced influence on groundwater chemistry.

Because it was not possible to sample boreholes or springs, the composition of true groundwater had to be inferred from streamwater samples taken during very low-flow conditions, as in long periods of dry weather (Figure 83). 'Groundwater' collected in this way had larger concentrations of calcium, magnesium and bicarbonate than soil water, but smaller amounts of aluminium. The calcium is thought to have been derived from small veins of calcite within the bedrock; the magnesium resulted from mineral weathering. The inclusion of these elements will tend to decrease water acidity, the release of calcium and magnesium

Plate 34 The Culm—an area of mainly grassland lying to the north of Dartmoor
(Photograph C J Barr)

Plate 35 The Culm is characterized by poor soils resulting in large areas being accorded Less Favoured Area status
(Photograph C J Barr)

Plate 36 The study is seeking to identify areas for potential wood production both from new plantations and from existing woodland
(Photograph C J Barr)

Plate 37 Laggan, Lochaber, Highland Region. Multiple land use presents a range of planning issues (Photograph T K MacKenzie, Highland Regional Council)

Plate 38 The rural land use information system developed by Highland Regional Council and ITE can be used to examine issues such as amenity woodland status and recreation pressures
(Photograph C J Barr)

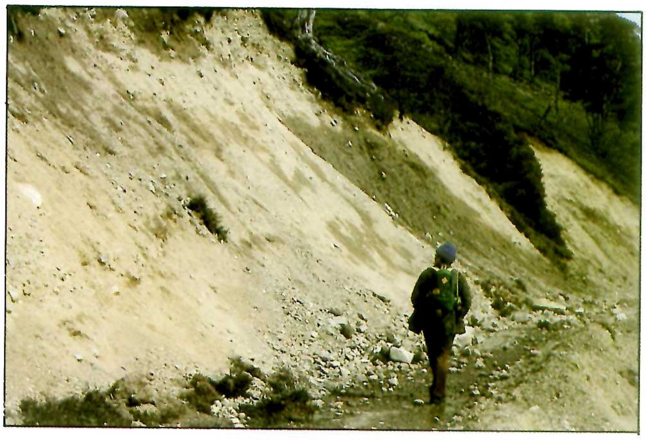

Plate 39 Bulldozed track within the Cairngorms National Nature Reserve, at Glen Feshie
(Photograph A Watson)

Table 33. Solute concentrations in soil 0 and E horizons, peat drainage and pipeflow (mg l^{-1} except pH)

Solute	0 horizon	Peat drainage	Pipeflow	E horizon
Na	2.69	3.0	2.84	2.77
K	0.66	0.18	0.24	0.20
Ca	0.39	0.40	0.23	0.42
Mg	0·52	0·51	0·37	0·47
Al	0·08	0·01	0·07	0·20
Si	0·35	0·16	0·39	0·89
No$_3$-N	0·09	0·01	0·07	0·25
SO$_4$-S	1·29	1·40	0·97	1·21
Cl	5·22	6·13	5·09	5·16
DOC	10·10	17·40	n.d.	3·94
pH	4·01	3·89	3·93	4·39

involving an exchange of hydrogen ions. The decreased amount of aluminium in the groundwater is attributable to its decreased solubility in less acid waters.

Assuming that incident precipitation moves through the different 'compartments' that have just been discussed, the following changes in composition can be conjectured. Starting with dilute, weakly acid precipitation dominated by marine-derived sodium, magnesium and chloride, and including sulphate, nitrate and calcium, the concentrations of these solutes and potassium are likely to increase on contacting vegetation: detectable amounts of silica would appear. While moving through soils, the generalizations are difficult to make; however, the concentrations of silica and dissolved organic carbon will predictably increase, as will those of aluminium. Reactions between soil water and bedrock will result in augmented concentrations of calcium and magnesium and decreased amounts of aluminium. Thus, much of the sodium, chloride and sulphate in streams will be atmospheric in origin, but bedrock sources may predominate for calcium. Potassium, silica and dissolved organic carbon will be mainly attributable to vegetation and soil.

Effects of flow rates on the composition of streamwater

If all incoming precipitation moved through vegetation, soil and rock before draining into streams, streamwater chemistry would be the same as that of groundwater. However, in most conditions, streams include a mix of waters from a variety of sources - groundwater, peat drainage, throughflow (horizontal flow) from stagnopodzols, pipeflow and overland flow (Bell 1972) - whose relative importance depends on amounts and intensities of rainfall and on antecedent conditions.

Groundwater is the only input to streams during long dry spells when flows are low, or during long cold spells when other potential inputs are frozen. During moister conditions, when streams flow faster, water from other sources, especially peat drainage, becomes mixed with groundwater. In thoroughly wet conditions, throughflow (horizontal flow) from stagnopodzols may become a significant input, with pipeflow increasing in importance when heavy rain falls on to already wet soils. Heavy rain in autumn and winter falling on to saturated soils can result in above-ground flow of surface waters. Each of these sources of water has a different chemical composition, and thus the composition of a stream will be determined by the proportions of water derived from each source. Overland flow probably occurs 2 or 3 times per year at the most, pipeflow on 10 to 20 days per year. Groundwater is probably the only contributor on 20 to 30 days per year.

In addition to the various inputs, water composition is influenced by seasonally varying amounts of nitrate and potassium which are usually largest in winter (Reynolds *et al.* 1983). Large sulphate concentrations may occur when organic sulphides are oxidized to sulphate after periods of drought. Concentrations of silica in the streams are inversely related to its uptake by diatoms which is maximal in late spring and early summer (Casey *et al.* 1981). Thus, although one can give general indications of sources of elements and factors controlling stream chemistry, a detailed study of a given flood may have to consider many factors, including sources contributing to the stream, chemistry of precipitation, season and antecedent conditions.

In summary, it is now possible to speculate about the exchanges occurring in the different compartments of a terrestrial ecosystem - vegetation, upper and lower soil horizons and bedrock - but the ability to predict quantitative, in contrast to qualitative, changes necessitates a much more comprehensive series of studies.

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MYCORRHIZAS AND THE GROWTH OF BIRCH AND SYCAMORE SEEDLINGS IN 25 CUMBRIAN SOILS

Most trees in the UK are naturally infected by mycorrhizal fungi which initiate either sheathing (ecto-) or vesicular-arbuscular (endo-)mycorrhizas. The importance of these mycorrhizas in nutrient cycling is no longer disputed, but our knowledge of the interrelationships between host plants, fungi and soil types in natural and semi-natural habitats is limited, primarily because most mycorrhizal research has been concentrated on crop plants usually growing in partially sterilized and/or highly fertile soils.

To help correct this deficiency, birch (*Betula pendula*) and sycamore (*Acer pseudoplatanus*) seedlings were grown in pots of 25 non-agricultural and unsterilized soils from a range of sites in Cumbria, including semi-natural woodland, carr and upland heath (Frankland & Harrison 1985; Harrison & Helliwell 1981). Both tree species are widespread in Britain, grow in a wide range of soils, and have potential uses on marginal sites – birch as a possible soil improver (Miles 1981), and sycamore for upland shelterbelts and as a species tolerant of pollution.

When the seedlings were 2 years old, amounts of mycorrhizas and the extent of plant growth were assessed. Most seedlings had become mycorrhizal, sheathing mycorrhizas occurring in birch, and vesicular-arbuscules in sycamore. Their occurrence, expressed as the percentage of root tips colonized, was significantly related to a range of soil properties – pH, organic matter content, total and exchangeable phosphorus and, unexpectedly, with amounts of extractable iron (Table 34i). Iron has rarely been implicated in mycorrhizal development: the correlation may reflect an indirect relationship with the availability of phosphorus, an aspect that needs further study. Seedling height and weight, and root surface area were significantly and directly related to the occurrence of mycorrhizas. Interestingly, the birch associations were stronger with 'immature' than with 'mature' mycorrhizas (Table 34i, ii), suggesting that the sheathing (ecto-)mycorrhizas were physiologically active at an early stage in their development. Sanders *et al.* (1977) suggested that plant growth is favoured by the early colonization of roots of mycorrhizal fungi.

In multiple regression analysis, 80% or more of the variation in seedling growth was attributable to combinations of soil chemical properties. Of what consequence, therefore, were the mycorrhizas to their host? The inclusion of observations about the occurrence of mycorrhizas in similar statistical analyses showed that mycorrhizas contributed in a small (approximately 10%), but significant, degree to the heights of birch, and to the heights and weights of sycamore.

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Table 34. Relationships (R^2) between the occurrence of mycorrhizas on seedling roots of birch and sycamore and (i) soil chemical properties and (ii) seedling growth

		Occurrence of mycorrhizas (% total root tips colonized)			
		Birch			Sycamore
		Mature	Immature	All ages	All ages
i. Soil properties					
pH		0·00	0·30*	0·29*	0·37***
Organic matter		0·07	0·10	0·11	−0·40***
Phosphorus	total	0·01	0·48***	0·51***	0·53***
	isotopically exchangeable	0·01	0·30*	0·32*	0·43**
Iron extractable in oxalic acid		0·19*	0·25*	0·30**	0·63***
ii. Growth attributes					
Shoot	height	0·03	0·57***	0·62***	0·73***
	weight	0·00	0·29*	0·31*	0·73***
Root	weight	0·00	0·31*	0·34*	0·79***
	surface area	0·00	0·35**	0·39**	0·78***

*, **, *** Significant at $P<0{\cdot}05$, 0·01 and 0·001 respectively

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DOES AFFORESTATION WITH SITKA SPRUCE AFFECT SOIL ORGANIC MATTER?

Organic matter often accumulates, particularly in surface soils (Jenkinson 1970; Turner 1981), and these accumulations are of economic importance on poor upland soils where nutrients are locked in organic complexes, so necessitating the application of fertilizers if tree growth is to be maintained. Although large areas of upland Britain have been planted with Sitka spruce (*Picea sitchensis*), little is known of the effects of this species on soil organic matter. Adams (1974) found that litter accumulations remained constant, whereas Carey and Farrell (1978) found that they continued to increase as forests age.

In order to assess the possible effects of Sitka spruce afforestation on upland peaty gley soils in NW England, samples of litter and topsoil (15 cm) were collected from stands of different ages (13 to 30 years) in the Bowland Forest during 1983. To allow for differences in soil bulk densities, the analyses of carbon content were expressed by volume. In the event, the carbon content of the litter layer rapidly reached a constant amount of approximately 7 kg cm^{-2}, which was slightly more than the amount in topsoil. The establishment of this constant amount indicates that the decomposition of forest floor litter was fairly rapid, and suggests that this process may release significant amounts of nutrients for tree growth, as suggested by Gessel *et al.* (1973).

Apart from the surface litter layer, it was not possible to detect increases in soil organic matter at greater depths attributable to afforestation. There are many possible reasons, including site variability, and, perhaps more significantly, a possibly slower rate of accumulation which only becomes discernible when plantations are more than 30 years old.

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ACID PHOSPHATASE PRODUCTION BY SHEATHING (ECTO-) MYCORRHIZAL FUNGI: ITS POSSIBLE ROLE IN NUTRIENT CYCLING

In the main, it has been thought that mycorrhizal fungi aid plant nutrition because their hyphae ramify and search larger volumes of soil than would be the case if plants had to rely on their own root hairs. The nutrients gained via mycorrhizas are thought to be derived mainly from inorganic sources (pools) maintained by the mineralization of litter organic complexes. This mineralization is largely attributed to decomposer (saprotrophic) microbes, but, because some mycorrhizal fungi possess enzymes such as phosphatases (Alexander & Hardy 1981; Ho & Zak 1979) and cellulases (Oelbe 1982; Linkins & Antibus 1981), it has been suggested that mycorrhizal fungi may accelerate litter decomposition (Plate 26). On the other hand, Gadgil and Gadgil (1975) suggested that mycorrhizal fungi compete with decomposer microbes for available nutrients.

The ability of sheathing mycorrhizal fungi to produce phosphatase has been compared with that of known decomposer basidiomycetous fungi when grown on artificial media (Dighton 1983). Phosphatase production was assayed when mycelial cultures were grown in Hagem's liquid medium, containing either an inorganic (orthophosphate) or an organic (inositol hexaphosphate (IHP)) source of phosphorus. The mycorrhizal fungi usually produced more acid phosphatase per unit weight of mycelium than the decomposer fungi *Mycena galopus* and *Marasmius androsaceus*. Because phosphatase production was independent of phosphorus concentrations, irrespective of the source of phosphorus (Figure 84), it seems that the negative feedback mechanism controlling the production of phosphatase by mycorrhizal roots of birch and pine may be a root-initiated, rather than a fungus-initiated, response. However, what happens to the phosphorus hydrolyzed from organic sources by mycorrhizal fungi? The role of mycorrhizas is to enhance nutrient uptake by roots, which, if it were to act in conjunction with the release of inorganic P from the organic sources, would require the hydrolyzed P to be freely available in the rhizosphere for plant uptake, or at least available in the fungal biomass for transport to 'host' plants. Two of the 3 mycorrhizal fungi examined (*Lactarius rufus* and *Paxillus involutus*) released considerably more inorganic P from the organic source (IHP) of phosphorus than the 2 saprotrophic basidiomycetes being studied (Figure 85). However, a greater proportion of the

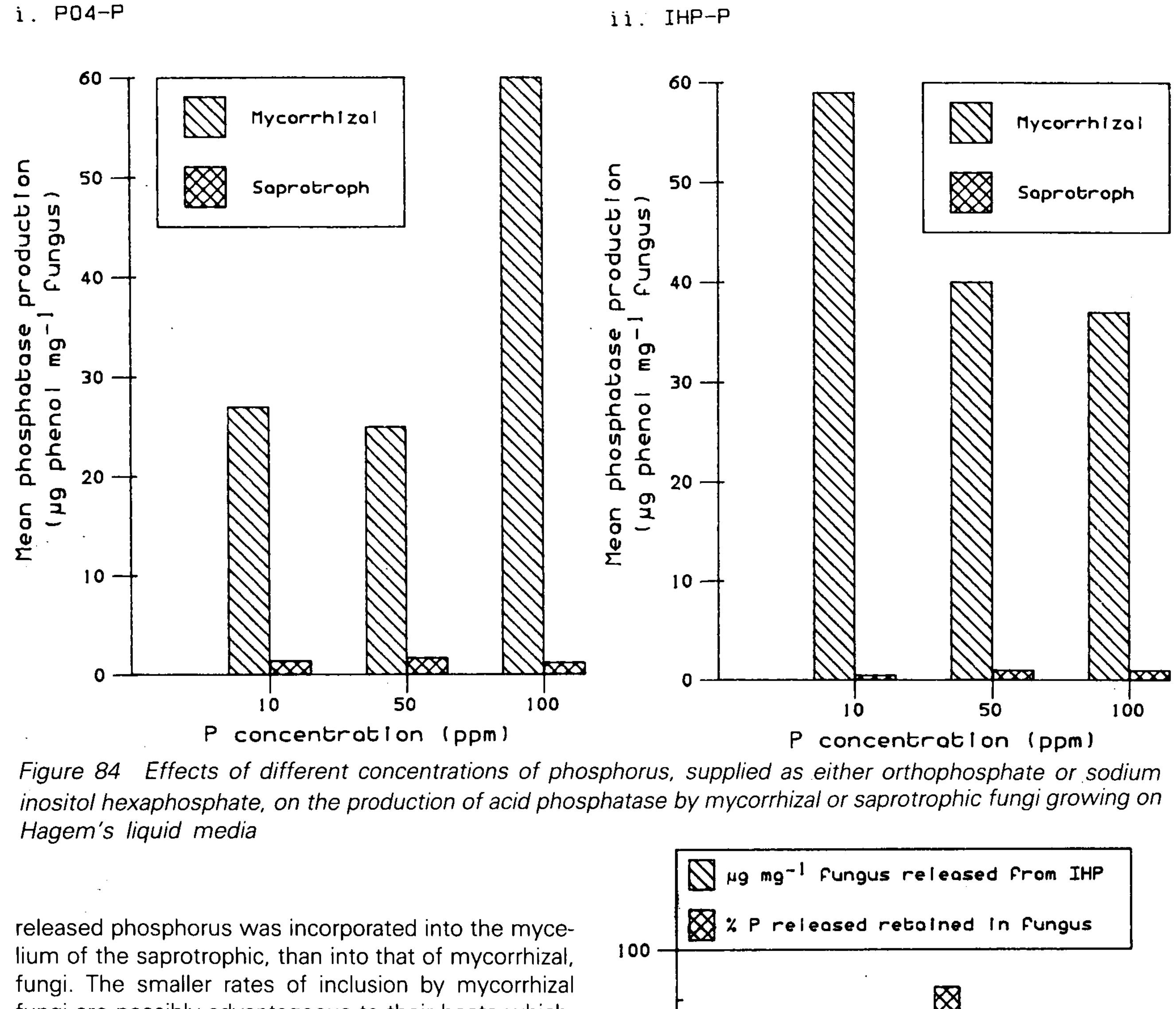

Figure 84 Effects of different concentrations of phosphorus, supplied as either orthophosphate or sodium inositol hexaphosphate, on the production of acid phosphatase by mycorrhizal or saprotrophic fungi growing on Hagem's liquid media

released phosphorus was incorporated into the mycelium of the saprotrophic, than into that of mycorrhizal, fungi. The smaller rates of inclusion by mycorrhizal fungi are possibly advantageous to their hosts which, as a result, have a larger 'pool' of phosphorus available. Unlike *L. rufus* and *P. involutus, Suillus luteus,* the third mycorrhizal fungus, behaved more like the saprotrophs than the other mycorrhizal fungi being studied.

Although the production of phosphatase varies between species of fungi, and among different isolates of the same species, the limited observations so far obtained support the hypothesis that mycorrhizal fungi produce significant amounts of phosphatase, releasing phosphorus in excess of their own requirements. This facility, combined with the ability to produce cellulase enzymes (and so drive energy), might enable mycorrhizal root systems to be less dependent on saprotrophic organisms than non-mycorrhizal root systems, a feature of possibly significant benefit in stressed environments, such as the Arctic where the temperature-dependent period of mineralization is short. The ability to produce litter-decomposing enzymes may be a feature of stress-tolerant mycorrhizal fungi, also of those fungi occurring late in the mycorrhizal successions associated with forest trees where organic nutrients accumulate (Dighton & Mason 1985).

J Dighton and M R Smith

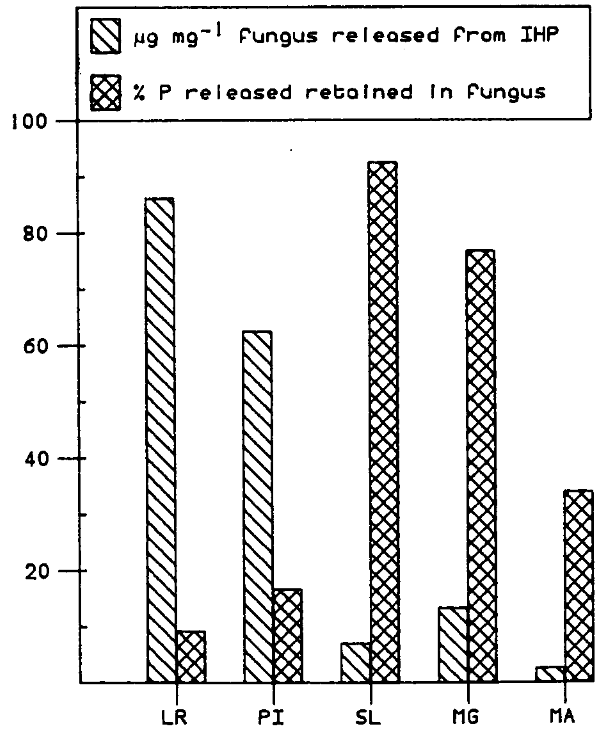

Figure 85 Release of inorganic P from inositol hexaphosphate and the percentages of hydrolized P incorporated into fungal mycelium when 5 basidiomycetous fungi were grown in Hagem's liquid medium. Lactarius rufus (LR), Paxillus involutus *(PI) and* Suillus luteus *(SL) form sheathing mycorrhizas;* Mycena galopus *(MG) and* Marasmius androsaceus *(MA) are saprotrophic*

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Programme 13
LAND RESOURCES AND LAND USES

RURAL LAND USE AND LANDSCAPE CHANGE

There is widespread interest and concern about the nature, scale, and rates of change in the rural landscape of Britain. Partly as a result of this concern, ITE is investigating methods for assessing quantitatively the present distribution of landscape features and different types of land cover so as to obtain a baseline for judging both past and future changes. The approach is based on studies already completed, in which data were obtained after stratifying the country into a limited number of land classes derived from multivariate analyses of map-derived geological, topographical and climatological data (Bunce *et al.* 1983).

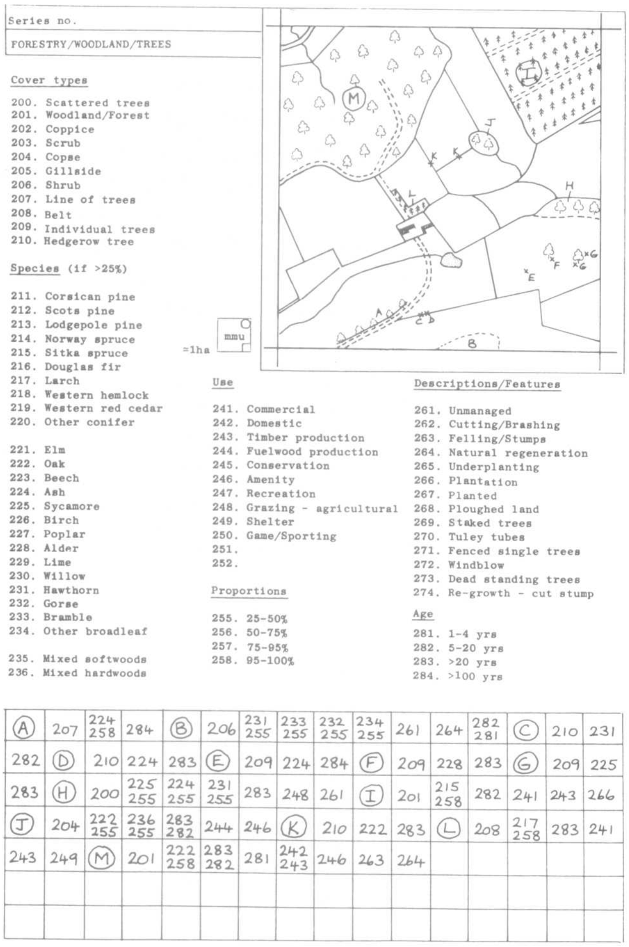
ITE project 899 – *Rural land cover and landscape change* – provides an 'umbrella' for 3 sub–projects. The first is a detailed field survey of 384 grid squares, each 1 km × 1 km – 12 random squares in each of the 32 land classes (ITE 909). The second (ITE 900) is concerned with a comparative study of colour air photographs (1 : 10 000) and field surveys as alternative or complementary sources of information. The third sub-project relates to the statistical aspects of (i) the sampling strategies used in ITE 900, and (ii) the extrapolation of data to national and regional evaluations. This report concentrates upon the first phase of the 2-year field survey (ITE 909).

To establish the date base, a survey was made during 1977 and 1978 of 8 replicate squares, 1 km × 1 km, of each of the 32 land classes into which Britain has been divided; types of ground vegetation and soil were recorded (Bunce *et al.* 1983). At the same time, types of land cover and the characteristics of some linear features (eg hedgerows, walls and fences) were mapped. With this valuable starting point, it was decided to arrange a repeat ground-based survey (monitoring) during the summer of 1984. This second survey was designed to meet a variety of objectives. It was to test our ability to design a method of sampling, using ground survey, which would provide reasonable quantitative estimates of landscape change over comparatively short periods of time (6 or 7 years), and, in so doing, give a reliable record of the current status of the British countryside.

Second, and subject to the results of the methodological study, it was to provide relevant statistics, with appropriate error terms attached, for the degrees of change. To allow the option of future partial replacement sampling (Ware & Cunia 1962), the number of sites surveyed was increased from 256 in 1977 and 1978 to 384 in 1984. To minimize the risks of seasonal variations, it was necessary to survey the sites in as short a time as was practical. Staff from 6 of the ITE stations were deployed within 3 months. Strenuous attempts were made to ensure that there were no inconsistencies between the survey teams. At an early stage, a joint field course was held to familiarize staff with field methods, including the use of a field handbook. During the summer, a project quality control team made regular visits to each of the teams in the field, so as to gain an estimate of recorder consistency – 2 squares were surveyed by all of the teams. The range of data recorded was based on the prior experience of members of staff, and as a result of discussions with other agencies concerned with landscape and the rural environment. An extensive list was prepared on the understanding that the different records might be combined in different ways to meet differing needs, a challenge which would be used as an arbiter when judging the merits of the method being used.

Observations were mapped (1:10 000 and larger) as areas, lengths or points, with supplementary records being entered into a booklet with separate pages for each of the subject areas, including (i) physiology, inland water and coast, (ii) agriculture and semi-natural vegetation, (iii) forestry, woodland and trees, (iv) boundaries, (v) recreation, and (vi) buildings, structures and communications. To describe mapped features as fully as possible, a system of multiple coding was used, each distinctive set of features being recorded on the relevant map using a letter, an 'alpha' character. Elsewhere on the recording sheet, alpha characters were described in terms of a predetermined list of numerically coded information. For example, the letter 'P' marked on the map might represent a copse (204) composed of ash (224), 50-75% (256), and sycamore (225), 25-50% (255), which was used for recreation (247) but was otherwise unmanaged (261), with trees i.

ii.



Series no.

FORESTRY/WOODLAND/TREES

Cover types

200. Scattered trees
201. Woodland/Forest
202. Coppice
203. Scrub
204. Copse
205. Gillside
206. Shrub
207. Line of trees
208. Belt
209. Individual trees
210. Hedgerow tree

Species (if >25%)

211. Corsican pine
212. Scots pine
213. Lodgepole pine
214. Norway spruce
215. Sitka spruce
216. Douglas fir
217. Larch
218. Western hemlock
219. Western red cedar
220. Other conifer

221. Elm
222. Oak
223. Beech
224. Ash
225. Sycamore
226. Birch
227. Poplar
228. Alder
229. Lime
230. Willow
231. Hawthorn
232. Gorse
233. Bramble
234. Other broadleaf

235. Mixed softwoods
236. Mixed hardwoods

Use

241. Commercial
242. Domestic
243. Timber production
244. Fuelwood production
245. Conservation
246. Amenity
247. Recreation
248. Grazing - agricultural
249. Shelter
250. Game/Sporting
251.
252.

Proportions

255. 25-50%
256. 50-75%
257. 75-95%
258. 95-100%

Descriptions/Features

261. Unmanaged
262. Cutting/Brashing
263. Felling/Stumps
264. Natural regeneration
265. Underplanting
266. Plantation
267. Planted
268. Ploughed land
269. Staked trees
270. Tuley tubes
271. Fenced single trees
272. Windblow
273. Dead standing trees
274. Re-growth - cut stump

Age

281. 1-4 yrs
282. 5-20 yrs
283. >20 yrs
284. >100 yrs

Ⓐ	207	224 258	284	Ⓑ	206	231 255	233 255	232 255	234 255	261	264	282 281	Ⓒ	210	231
282	Ⓓ	210	224	283	Ⓔ	209	224	284	Ⓕ	209	228	283	Ⓖ	209	225
283	Ⓗ	200	225 255	224 255	231 255	283	248	261	Ⓘ	201	215 258	282	241	243	266
Ⓙ	204	222 255	236 255	283 282	244	246	Ⓚ	210	222	283	Ⓛ	208	217 258	283	241
243	249	Ⓜ	201	222 258	283 282	281	242 243	246	263	264					

Figure 86 i. An example of a landscape
ii. A page from the recording booklet, showing coding of some woodland features

aged 5-20 years (282) and over 20 years (283) (Figure 86). In due course, this approach might lend itself to the use of hand-held data loggers.

In addition to the ground observations, the surveyors were asked to take a series of colour transparencies at each site and to note information given by occupiers. The latter might help socio-economic interpretations of change, while the former may provide a basis for ground photography monitoring, in addition to forming a series of representative landscape pictures. With the 1984 survey completed, the project is now in the measurement and analysis phase. The new information is being digitized and transferred to computer file, the data base being structured to allow maximum flexibility, including a variety of approaches to modelling, such as linear programming (see Bishop 1978; Bunce *et al.* 1984). It should be possible to identify the extent of recent landscape changes both regionally and nationally, but how much effort must be expended to obtain results with a high degree of certainty?

C J Barr, D F Ball, R G H Bunce and Heather A Whittaker

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POTENTIAL FOR WOOD PRODUCTION ON THE CULM MEASURES

(A subcontract done by ITE for Dartington Institute which is funded by the Commission of European Communities, in addition to MAFF, FC and CC)

The Culm Measures, 3100 km^2 in extent, are situated in north Devon in south-west England (Plates 34 and 35). ITE has been subcontracted to produce (i) a land classification of the area and (ii) a predictive model to estimate the potential for afforesting. As such, this is a relatively small contribution to the overall project for which the Dartington Institute is responsible. Overall, the project aims to establish the regional potential for wood production from existing forest stands and from afforesting agricultural land within the context of efficient farming (Plate 36).

The area of the Culm has been allocated to 11 land classes, arranged by classifying map-readable records of climate, soil, topography and human artefacts taken from a quarter of the 1 km squares on the Culm; the data were classified using the procedure described by Bunce *et al.* (1983). Although it was thought that differences in climate would be relatively unimportant in this study of a restricted area, they proved to be dominant. Accordingly, a second classification was evolved, this time omitting climatic attributes. However, the basic structures of the 2 classifications were similar, with altitude in the second classification acting as a surrogate for climatic factors. Because the risk of windthrow strongly influenced forest practices, and because it is related to climate, it was decided to use climatic factors in completing the classification of all the squares.

One hundred squares, including the range of land classes, were then selected at random and surveyed by 2 sets of field surveyors using procedures and handbooks prepared by members of ITE. They recorded and mapped, on 1:10 000 maps, the following attributes:

1. agriculture: occurrence of crops and semi-natural vegetation; details of soils and estimates of the potential for improving agricultural production;
2. forestry; volume estimates in sample plots in every block of woodland in the 100 squares sampled; records of current state of forest/woodlands.

These data have been assembled and the units of land have been labelled within each square (Figure 87) using the procedure described by Bunce *et al.* (1981). The institutional constraints, eg Local Nature Reserves and patterns of potential afforestation, have been superimposed upon the distribution of agricultural land uses. The areas of the different units have been measured, and a microcomputer program written to produce a model which can examine competition for land between forestry and agriculture in a variety of 'scenarios', the financial implications being examined according to the procedures described by Mitchell *et al.* (1983). The prospects of agricultural improvement are being examined so as to assess the sensitivity of the model to changing farmland practices. Similarly, the significance of different silvicultural techniques is being investigated.

R G H Bunce, C J Barr and Heather A Whittaker

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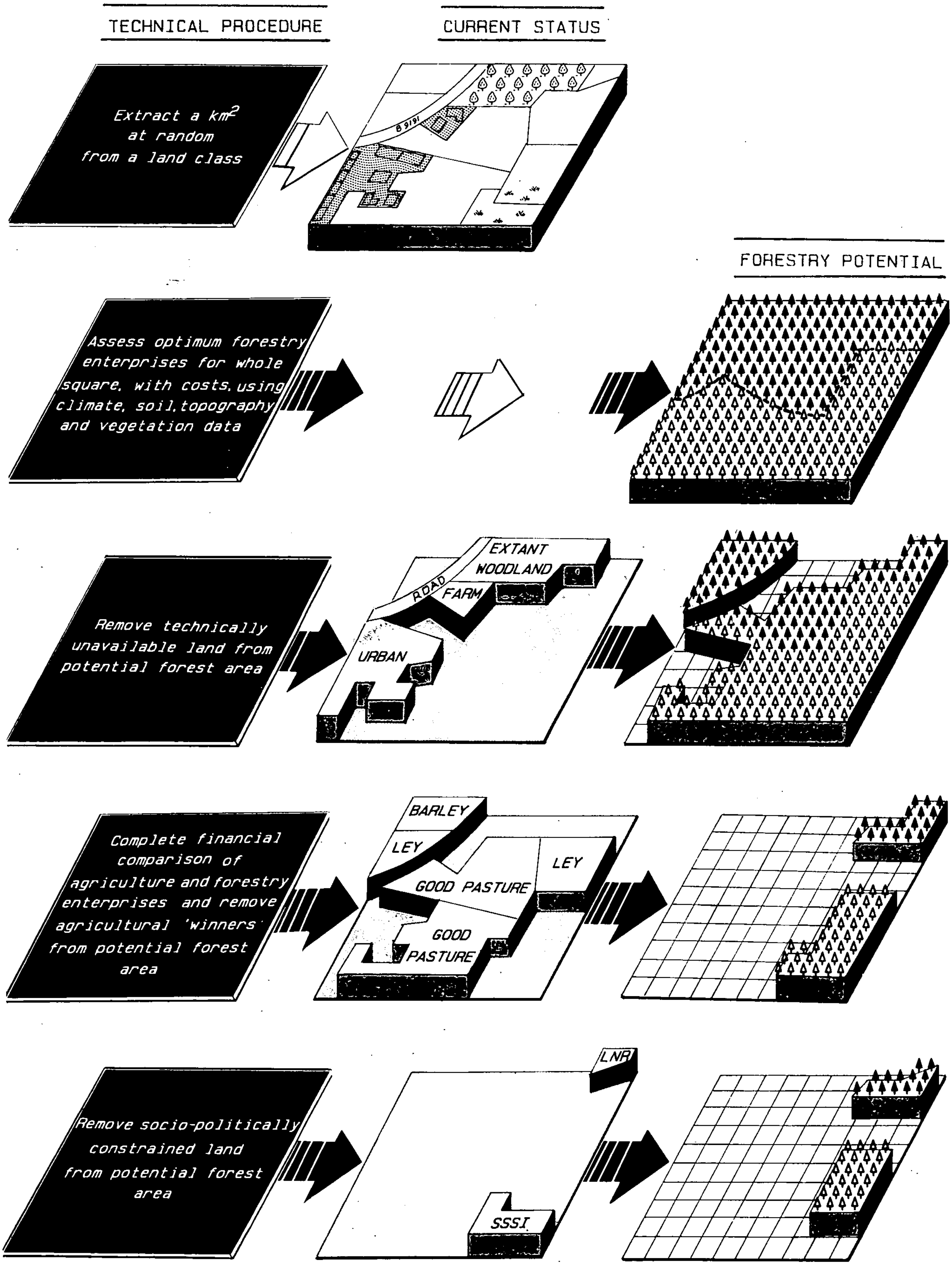

Figure 87 Example of estimation of forestry potential in 1 km squares

THE DEVELOPMENT OF A RURAL LAND USE INFORMATION SYSTEM - AN EXAMPLE OF CO-OPERATION BETWEEN ECOLOGISTS AND PLANNERS

(This work was supported by Highland Regional Council, Scotland, funds)

During the last 3 years, members of ITE have been working with the Planning Department of the Highland Regional Council to produce a rural land use information system. The Region measures 25 391 km^2, is generally 'upland' in nature (Figure 88), and has a population of less than 200 000 – it is thus predominantly rural. Inevitably, therefore, the Planning Department is strongly concerned with the Region's environment, much of it remote, and with issues such as rural depopulation and afforestation (Plate 37). It needs to be adequately informed so that it can stimulate new patterns of land use and test policy options. Although agencies such as the Forestry Commission and the Red Deer Commission have extensive data relating to the Highland Region, these data are not held in a consistent format enabling ready access and cross-reference. It has therefore been necessary to establish a unified inventory of regional statistics involving all aspects of land use, including geographical distribution and predicted, in addition to actual, land uses. With these data, it should be possible to consider and guide future changes: data also provide a basis for comparing the impacts of different environmental changes whether related to afforestation, agricultural improvements, or other rural systems.

The development of the information system has been based upon the Merlewood land classification system (Bunce & Heal 1984; Bunce *et al.* 1981). This classification method provides a sampling technique that enables the acquisition of rural land use information, and a variety of data, including demographic variables.

At the start of the Highland Region/ITE collaborative study, there were 2 main aims: (i) to allocate a quarter of the 1 km^2 of the Highland Region to the 32 GB land classes, which were to be subdivided where appropriate, and (ii) to make detailed field surveys of 8 randomly selected squares of each of 10 classes and 14 sub-classes (Bunce *et al.* 1984; Highland Regional Council 1985).

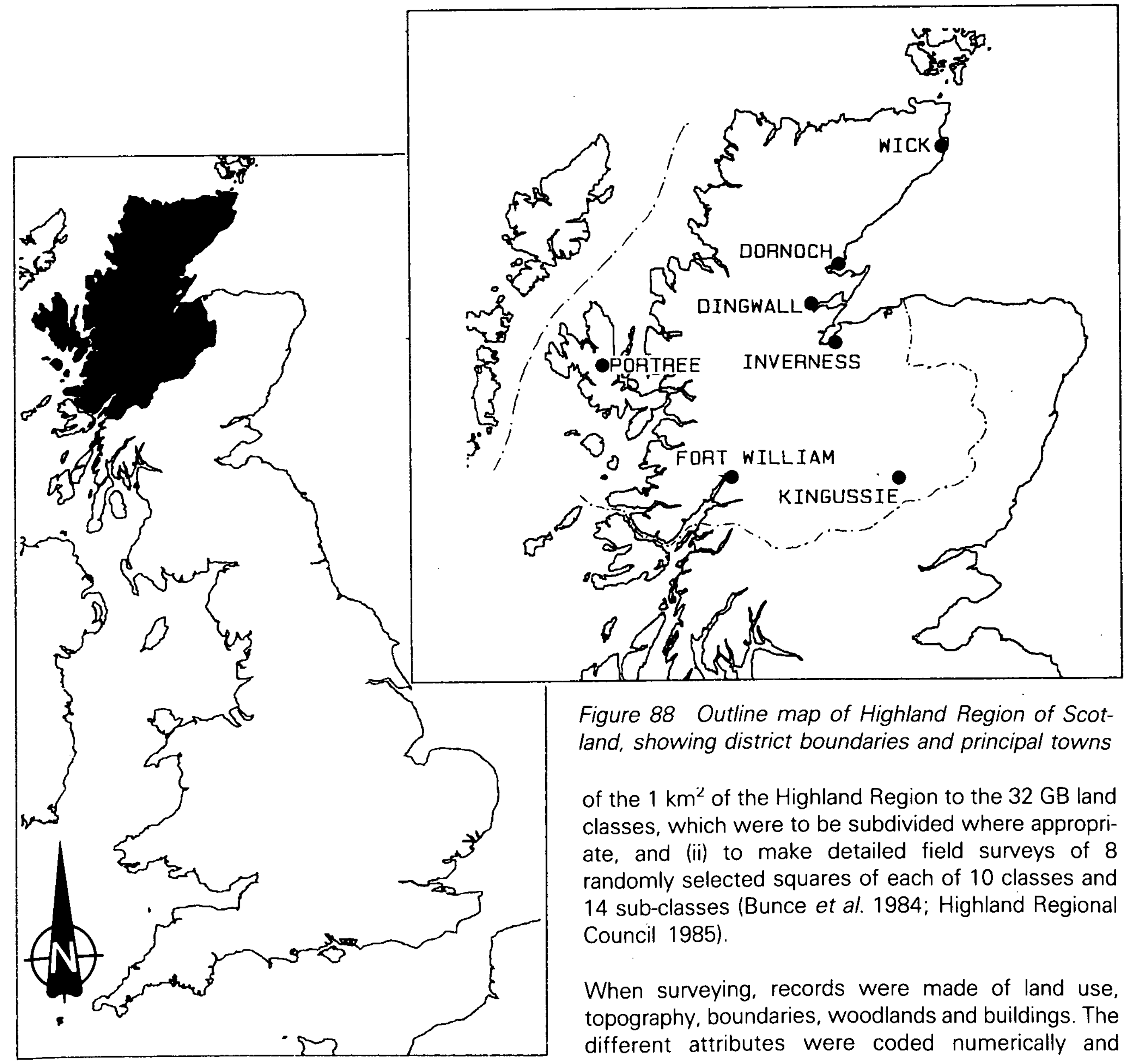

Figure 88 Outline map of Highland Region of Scotland, showing district boundaries and principal towns

When surveying, records were made of land use, topography, boundaries, woodlands and buildings. The different attributes were coded numerically and marked on to 1:10 000 maps: when more than one aspect of a boundary or building was noted, eg the species and height of trees, then the strings of numerical codes were represented by a single letter (A, B, ...), enabling complex data to be readily transferred to a computer and interrogated.

In the second year, the 'team' of ecologists and planners was concerned largely with processing field data and developing procedures for assigning the remaining squares of the Region to classes and sub-classes. Initially, this analysis was attempted by hand. However, it was subsequently seen to be advantageous to record all data, thus enabling errors to be checked more easily, as well as building up an independent data base, and so the team switched to a computer-aided method of classification. As a result, it was decided to classify every square in the Region to obtain complete coverage. With the assembled data, 3 sorts of presentation can be made for the entire Region:

i. maps of individual attributes, eg altitude, areas of woodland, etc (Figure 89);
ii. maps showing the distribution of different land classes and sub-classes evolved using series of geological, topographical and climatological data (Figure 90);
iii. maps showing land use potential (eg land available for afforestation (Figure 91).

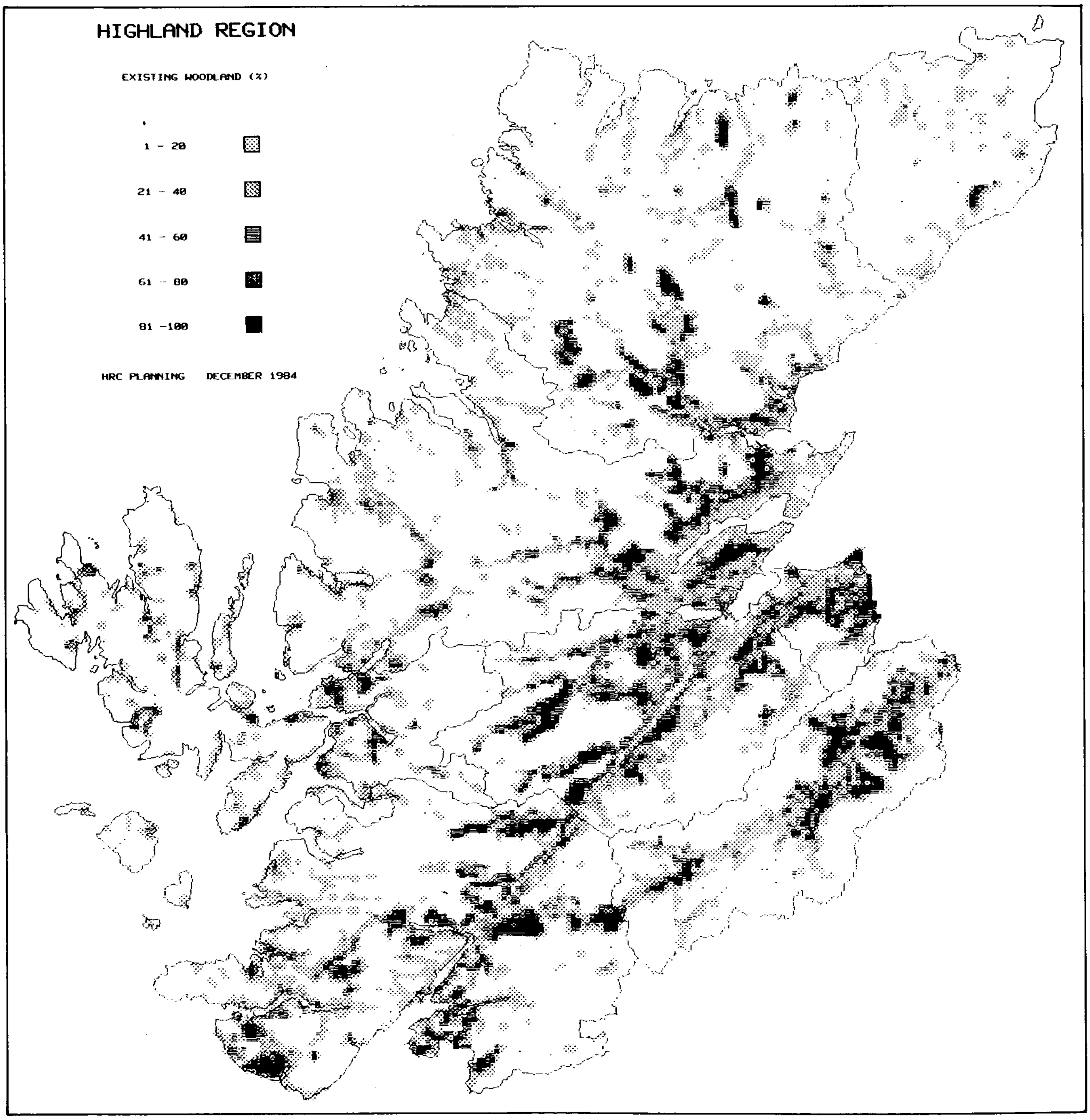

Figure 89 Distribution of areas of woodland, both broadleaved and conifer, in 1 km squares of the Highland Region, as recorded from 1:50 000 maps

During the third year, it has been possible to compare actual land uses recorded while surveying, with potential land uses predicted from the habitat characteristics of each land class or sub-class. For example, a model has been produced which enables the relative financial returns from agriculture and forestry to be examined for each sample square in each land class. By knowing exisiting land uses and the relative financial returns, it is possible to deduce how much land could be converted profitably, for instance to forestry, in each land class, and hence for the Region. To enable this deduction to be done expeditiously, the team has developed a series of equations, or algorithms, which allocate the forest potential to those squares in which land is available.

In 1984, the Regional Council decided to complete a woodland survey using the squares from the initial field sample that contained woodland, because the Region was particularly concerned with the loss of broadleaved woodland; it was also uneasy because it did not have a systematic study of its overall resource of trees (Plate 38). The objectives of the survey were to establish the economic, ecological and landscape significance of woodland in the Region, and to assess its state and the factors affecting its management. Likely changes also needed to be identified, and the potential for action to ensure continuity. Observations were therefore made of blocks of woodland, in addition to individual and small groups of trees. Records were made of tree diameters and heights (for volume estimation) and also of tree health.

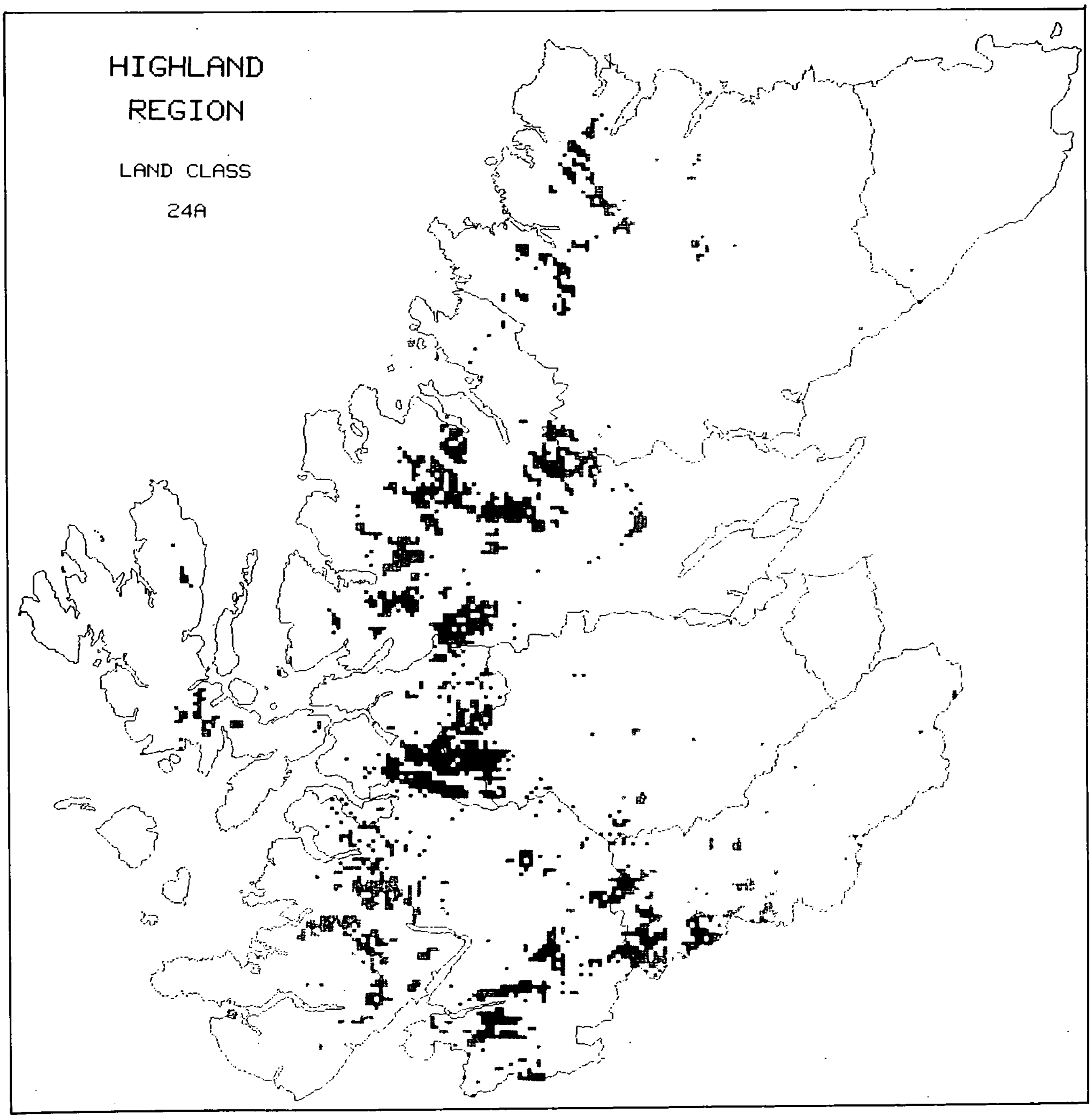

Figure 90 Distribution of sub-class 24A in the Highland Region of Scotland. This sub-class contains squares with steep slopes and rocky summits mainly in the south and west of the Region. The scenery is rugged with precipitous slopes covered by rough grass and heather moorland with sub-arctic vegetation at higher levels.

Early results have shown that the estimates of forest areas in the Region correspond to those produced independently by the Forestry Commission.

Contrary to expectation, birchwoods are regenerating widely, albeit often outside existing sites. Policy woods are shown to be declining – they are mainly composed of older trees, with few recent replacements. Several other categories, eg riverside trees, also show unbalanced age structures, and the survey has identified areas where action is required. Two reports have recently been published presenting the results of the survey.

The use of simple map-readable data has enabled an extensive date base to be constructed for the Highland Region in Scotland. It contains details of actual land uses and data of a range of environmental attributes, the latter enabling land use potential to be predicted. Thus, maps of predicted potential land uses can be prepared rapidly and cheaply.

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(*Highland Regional Council)

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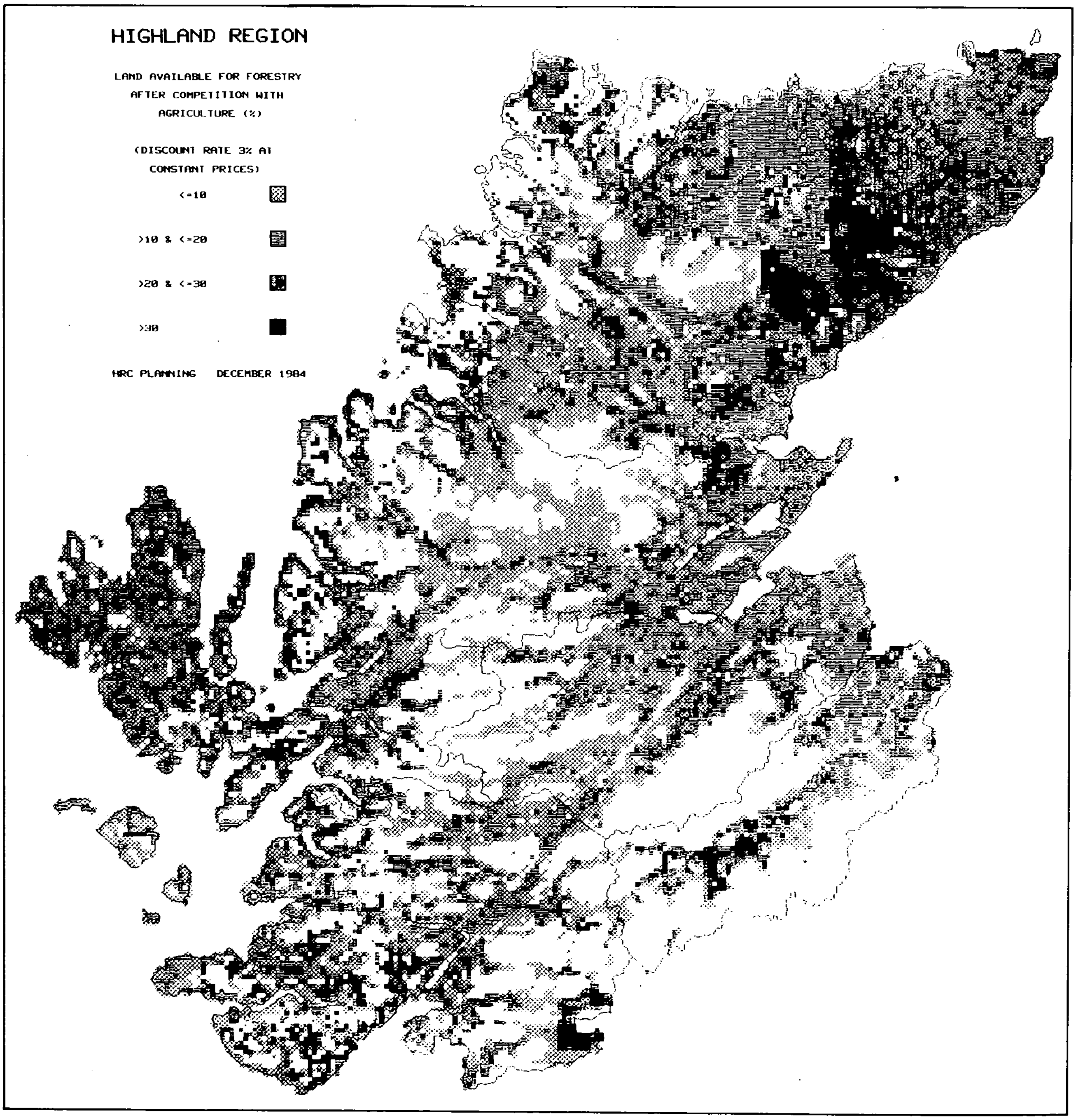

Figure 91 Distribution of the area of land technically available for new afforestation, in 1 km squares of Highland Region

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SPREAD OF BULLDOZED HILL TRACKS IN NORTH-EAST SCOTLAND

Since 1960, many rough hill tracks have been bulldozed on grouse moors and deer forests in eastern parts of Scotland, to ease access for vehicles carrying shooters. Hill walkers and others have complained that many of the tracks have destroyed former old footpaths, and also that the scars left by the tracks on open hillsides spoil the scenery and are major intrusions on wilderness areas. Most tracks have been cheaply made, below the standards for agricultural and forest roads, with inadequate drains and with spoil heaps left on the side of the tracks.

Within all National Scenic Areas designated by the Countryside Commission for Scotland (1978), landowners wishing to bulldoze hill tracks above 300 m have, since 1980, been obliged to obtain planning permission from the District Councils (Scottish Development Department 1980). Permission has been granted more than once in the Cairngorms (Plate 39) and at Loch Lomond. In addition to criticizing these developments, hill walkers and some planners regret that the need for planning permission applied neither to land below 300 m within National Scenic Areas nor to the great majority of hill ground outside them. A conflict has developed between the interests of shooters and of those concerned with the scenery and wild country which attracts many tourists to the area.

In response to interest shown by the Department of Physical Planning, Grampian Regional Council, a survey was made in 1981-82 of bulldozed hill tracks in Grampian Region and adjacent parts of Highland and Tayside Regions (Watson 1984). The data obtained have been incorporated into 1:50 000 scale maps (Grampian Regional Council 1984).

Of the 1151 km of new tracks found during the survey in Grampian Region, 32 km were in National Nature Reserves, 58 km in other Sites of Special Scientific Interest, and 156 km in what are now National Scenic Areas. Thirty per cent of the total were simply wheel tracks, on smooth, well-drained ground where vehicles could travel without preparation by bulldozing. Nine

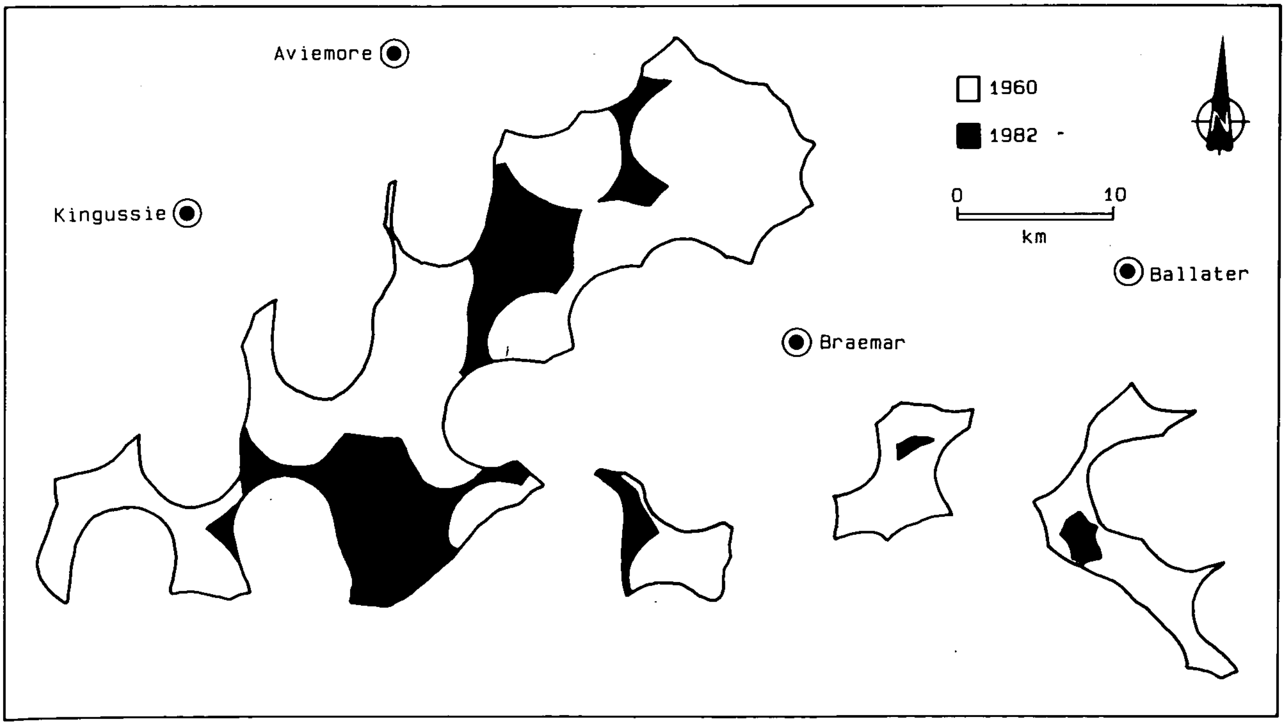

Figure 92 Decrease in area >3·2 km (2 miles) from the nearest road or vehicular track, 1969-82

per cent have been bulldozed on former footpaths, while 49% were entirely new alignments. While some of the new tracks extended to arctic-alpine ground at 1000 m or higher, most of the 16% of new tracks for non-sporting purposes (consisting of forestry, farming, hydro-electricity and radio-communication) were at low altitudes. Interestingly, lengths of bulldozed track were related to types of land ownership. Within the Grampian Region, there were respectively 306, 64 and 0 m of bulldozed track per km^2 of grouse moor owned by absentee landlords, resident landlords and the institutions.

As a result of these developments in the Grampian Region (plus adjacent hill ground in Highland and Tayside Regions), the area more than 3·2 km (2 miles) from the nearest vehicular tracks has decreased from 678 km^2 in 1960, to 154 km^2 in 1982, a significant loss of wilderness also associated with increased fragmentation (Figure 92).

A Watson

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Programme 14
CHEMICAL AND TECHNICAL SCIENCES

This Programme is mostly concerned with service work but, because the variety of requests received is so extensive, there is a need for a research and development background. The largest of the service sections is analytical chemistry which is now based entirely at Merlewood. The Monks Wood analytical chemists, previously included in this Programme, were transferred early in the year to Programme 8 (Ecophysiology and pollution in animals) because their work was almost entirely generated by that Programme. Their expertise remains, however, available for others, if appropriate.

Engineering is the only service group with members at most of the stations. Monks Wood, Merlewood, Bush, Brathens and Bangor all have an engineer available on station, although Furzebrook and CCAP still have no local support. The central engineering unit at Bangor exists to back up the station engineer, and also for larger, more complex jobs. The Bangor location is especially beneficial for the microprocessor application work because of the computing experience at that station.

The plant culture group is based entirely at Bush, where most of the plant growth and physiological research is based. Although little work is done by this group for staff elsewhere, the skills and facilities they possess can be drawn upon if necessary. The smallest of the services is the photographic unit, a one-man unit, which nevertheless caters for requests by staff throughout the Institute. Earlier this year, a biochemistry laboratory was set up at Furzebrook. Although not strictly a recognized service section, a description is included in this report because the specialities provide a service to staff at the station using electrophoretic techniques.

An NERC service, the mass spectrometer unit, is based at Merlewood. This unit was established to provide a stable isotope analytical service for NERC Institutes and grant-aided university workers. The unit is associated with the Chemical and Technical Sciences Programme for convenience, and a brief description of its work is given later in this report.

PROGRESS REPORTS OF THE SERVICE SECTIONS

Analytical chemistry (H M Grimshaw, J A Parkinson, J D Roberts, A P Rowland)

The demand for chemical analyses during the year greatly exceeded the resources and facilities available within the Merlewood service section. Such demands create conflicts between the need for high sample throughput and the need to maintain analytical quality, further aggravated by having to spend time on equipment maintenance and development of new methods. In the past, a continual process of review, improvement and rationalization has enabled the section to adapt to the Institute's changes in research. During the last 2 years, however, water samples from the research study sites have increased markedly to almost 10 000 samples a year. Two new projects in particular (ITE 625 and 841), concerned with the effects of clear-felling and acid rain, have been mainly responsible for this increased demand, although there are now 11 separate research studies in the Institute supplying waters to the chemical section. Inevitably, there have been fewer soil and vegetation analyses completed, but small blocks of samples take longer to process in real terms, and therefore a reduction in sample numbers creates other problems in an automated laboratory.

Many of the methods which are used for monitoring labile components in natural waters, such as preservation, rapid analysis and quality control, were well understood beforehand, but other factors have only become apparent as projects have developed. The different types of water which are analysed offer considerable variation in matrices, from the relatively low background of rainfall and streamwaters to samples such as soil lysimeter solutions, tree throughfall and stemflow which contain soluble, high molecular weight organic compounds. Seasonal and between-plot variation affects the determinand and matrix, which often makes the choice of analytical range difficult.

Changes in methods to accommodate new sample types have had far-reaching consequences on existing programmes, and recently there have been 3 major improvements which, although of some benefit, have so far failed to realize the expected increase in production. In the first development, a lower detection limit was achieved as a result of modifying the Auto Analyzer phosphate method, and this modification dramatically improved the quality of data. On the other hand, it meant that 2 concentration ranges had to be introduced into the procedure because the levels of phosphate in all solution types are so variable. A further modification was introduced to increase the tolerance of the nitrate method to organic interference. These interferences become apparent in samples collected in the April/May period which contain much higher levels of humic and fulvic fractions, especially in soil lysimeter solutions. To understand the method bias on previous data, it was necessary to run the 2 methods concurrently, whilst absolute recovery had to be monitored closely.

Ion chromatography appeared to be a good alternative technique for anions. It had particular advantages for sulphate analysis, whilst also giving results for nitrate, chloride and other anions. Automated equipment was installed at the beginning of the year and the evaluation showed good agreement between ion chromatography and previous methods. Unfortunately, installation problems, column performance, matrix effects and associated development have so far delayed the full implementation of this technique. Although it works well for waters with low organic content, the technique is less straightforward for many of the samples entering the laboratory, such as soil percolates and tree throughfall solutions.

The shift in emphasis from a traditional analytical to a mechanistic approach has led in a few instances to the customer placing a slightly different interpretation on the data provided by the service. In these circumstances, the procedures may not fulfil customer requirements until a better understanding of methodology is achieved; pH determination is a typical case which illustrates this point. The limitations of the method were acceptable when this parameter was used as a descriptive variable. However, there is now a need for more analytical awareness because results are used for hydrogen ion budgets in the acid rain studies, and it is especially important if pH tests are carried out in the field. For example, when dealing with solutions of low ionic strength, choice, care and storage of electrodes are important and the correct choice of buffers and meters is essential.

Aluminium analysis is another topic which has involved method development for acid rain studies. Labile fractions have recently been associated with increases in acidity in sensitive areas, and methods have been developed in conjunction with a colleague at Monks Wood to isolate toxic fractions.

The programme of method application tests was continued during the year. Tests showed that the sulphuric acid-hydrogen peroxide digestion procedure was suitable for the determination of both total nitrogen and phosphorus in most soils. Fusion and HF digestion techniques to recover aluminium and silicon from soils were also re-examined. Other new developments in the year included the modification of a method for formalin in peat extracts, and calibration of the X-ray fluorescence method for sulphur in a wider range of vegetation.

The on-line data processor, which has been in operation for 7 years, was replaced in 1984. Three linked processors and a microcomputer now share the tasks previously allocated to a central processing unit. This development has allowed more efficient operation of data collection and improved the customer report and computation facilities.

Engineering (G H Owen)

The engineering section continued to provide support for the research teams during 1984 and, although the trend was toward smaller tasks, it was possible to undertake a few major constructions. Financial stringency, experienced again this year, meant that much repair and modification of exisiting equipment were necessary.

The engineer at Monks Wood was fully occupied with requests for support, mainly for maintenance and repair work in the mechanical engineering field. During the year, it was possible to develop and construct a device for measuring the shape of eggs (ITE 289) and a root washing machine (ITE 602), both of which proved to be very effective.

At Merlewood, the construction work ranged from woodworking jobs to microprocessor applications. Most of the requests were for minor items, but one or 2 major tasks, for example a new glass-roofed growth room with refrigeration and electrophoresis equipment, were also completed. Other major jobs included a freeze concentrator (see p 146) and a new design of rain gauge cover for pollution studies.

Engineering work at Bush was roughly divided between looking after the glasshouses and growth chamber facilities on the one hand, and the requirements of the pollution programme on the other. A mobile laboratory for pollution field work was fitted out with all services, and support for the experimental complex at Glasgow continued. Building maintenance and alterations at Bush were successfully carried out during the year, with assistance of temporary staff employed under the MSC scheme. The engineer at Brathens, the second Scottish station, spent almost all of his time constructing radio-tracking equipment for the animal autecology projects.

All 3 engineers at Bangor were involved in preparations for the Open Day in October, both in relation to the engineering display and providing assistance generally. The central engineering unit continued to give support to the airborne and acid rain pollution projects at Bangor, developing dosing and sampling instruments and maintaining analytical equipment used in these studies. Specialized instruments for monitoring acid rain and for activating stream monitoring and sampling equipment have also been developed and built (see p 146). The station engineer was particularly involved in maintaining the controlled environment facilities and laboratory bench instruments.

Plant culture (R F Ottley)
Almost all the practical work was carried out at Bush, where most of the ITE glasshouses and nursery facilities are situated. Some of the culture experiments were carried out for staff elsewhere, and visits were made to other stations to provide advice on plant culture topics and landscape design.

The mist propagation equipment in the glasshouses, previously controlled by leaf surface moisture sensors, has been altered radically. With the help of the engineering service, a single control box for all 3 mist benches was developed to control the frequency and duration of misting. Initially, the system needed periodic adjustment to compensate for weather changes, but it now provides infinitely variable humidity regimes to meet the various demands of different species, eg a higher humidity for Sitka spruce (*Picea sitchensis*) than for *Pinus* spp.

The mist propagation benches were used intensively during the spring and summer, with a throughput of 10 000 cuttings of various species, including Sitka spruce, lodgepole pine (*Pinus contorta*), *Nothofagus* spp., birch (*Betula* spp.) and western red cedar (*Thuja plicata*). A large number of evergreen ground cover plants were also needed for landscaping purposes, which meant the benches were in constant use throughout the winter.

A major change in glasshouse practice during the year has been in the use of potting composts. Hitherto, it has been possible to use a 'universal' compost for most purposes, but this year it has been necessary to increase the use of 'field soils' and to add large amounts of sand, grit and perlite to facilitate the recovery of complete root systems. One consequence of this change was that different watering and feeding routines had to be introduced for the various composts.

All the available field plot areas (10·2 ha) were planted by the end of the year with research or experimental material, and any remaining corners were pressed into use for clone banks or plantings which did not call for any statistical design. A small area was returned to the Institute by the Department of Forestry and Natural Resources of the University of Edinburgh. All new plantings were completed in April into a prepared seedbed. The sowing of grass seed was withheld until late May to allow the young trees to establish before sward development. Because of the dry summer, the grass seed did not germinate until August. Approximately 90% of the field plots are now under a low maintenance rye-grass sward which requires infrequent mowing. About 1000 m^2 are close cut and the mowings removed to provide a clean short sward for mycorrhizal toadstool scoring. These areas require mowing in season every 1-2 weeks. Maintenance around the trees was minimized by the use of bitumin enclosure mats and by spraying under conifers with glyphosate in early autumn.

The nursery unit was involved in 3 landscape planting tasks during the year. In November, a small tree planting contract was carried out, which involved providing a screen around an area of coal mine waste. Following earlier successes in trials, 50% of the 3000 trees that were planted were alder (*Alnus glutinosa*). The perimeter was undersown with gorse (*Ulex europaeus*) and sea-buckthorn (*Hippophae rhamnoides*). At Monks Wood, the area around the new headquarters building was landscaped and planted with mainly indigenous species compatible with the rural setting. A scheme for future landscaping around the rest of the station was also designed. At Bush itself, bulk propagation of locally grown shrubs and ground cover was started in the summer for eventual planting around the new laboratories.

Photography (P G Ainsworth)
The demand and variety of work requested from the photographic service unit were well maintained in 1984, not least because of Open Day requirements. Most of the work carried out by the unit involves the production of prints for research and publication, including colour prints from colour slides and negatives, and both pictorial and diagrammatical slides to illustrate lectures and talks. In order to give a greater choice in the variety of lecture slides available to staff, a new technique was devised to produce colour slides of diagrams and tables, which made use of existing material, but incorporated a separate chemical treatment.

Colour prints, using both the 'Cibachrome' and 'Ektaprint' methods, and enlarged black and white headlines, captions and text were produced for display at seminars, symposia, conferences, agricultural and horticultural shows, and for Open Days held at Bangor and Monks Wood during the year. It has also been possible to use photographic techniques to aid design and layout, and to produce camera-ready artwork for publication covers.

There was some disruption to the work of the unit towards the end of the year, caused by the move from the temporary accommodation into a purpose-designed photographic suite situated in the newly constructed laboratory block at Monks Wood. The increased space available, and the acquisition of some extra studio lighting have eased the problems previously encountered in photographing equipment and specimens.

Biochemistry laboratory (Paulina E M Benham)
Earlier this year, a biochemistry laboratory was commissioned at Furzebrook to provide a base for the users of electrophoretic techniques.

The laboratory has been completely refitted with peninsular and wall benching, storage units, sinks and power points. A fume cupboard was installed with an extra hood over the adjacent balance bench to be used in the event of a spillage of fine-particulate chemicals. The addition of an automatic still provides the laboratory with a constant supply of single-distilled water.

The media used for electrophoresis range from starch and polyacrylamide gels to cellulose acetate strips. These gels are normally subjected to an electric current for 2 to 4 hours. Depending on the voltage used, the gel may become quite warm, producing distortions along the solvent front, unless adequate precautions are taken. Therefore, the tanks in which the current is applied to the gel are situated in refrigerated trays (similar to those used for keeping bottles ice-cold in public houses). Special shelving has been mounted on one wall in the biochemistry laboratory in order to accommodate 2 of these trays and the required number of power packs.

Other items of equipment include fridge/freezers for the storage of samples and chemicals and an incubator in which isoenzyme assays are usually developed at a temperature of 37°C.

Electrophoresis is regularly used by several members of staff to determine genetic variation within and between natural populations of a variety of organisms. Material examined includes *Spartina* spp., *Sphagnum* spp. (especially the *recurvum* complex), the *monticola* group of *Pardosa* wolf spiders, *Lasius niger* and *L. alienus* plus the hybrid.

At the moment, the laboratory facilities are being used by visitors from the Free University of Amsterdam and the Institute of Botany, Stockholm University.

NERC mass spectrometer unit (C Quarmby)
In the past few years, there has been a marked increase in the interest shown in the use of stable isotopes as an alternative to radionuclides for labelling purposes. This increased interest is particularly true for nitrogen, and consequently a laboratory has been established by NERC at Merlewood to provide an analytical service for those scientists using ^{15}N in the terrestrial and freshwater life sciences. There is a possibility of extending to other isotopes in the future.

A SIRA 9 mass spectrometer, a microprocessor-controlled version of the VG Micromass 903, has been installed, together with ancillary equipment necessary to process the samples. These samples will be sent to the laboratory in the form of dry ammonium salts and converted to nitrogen gas by means of the Rittenberg reaction. The laboratory is now in full working order, although considerable difficulties were experienced before the instrument was finally commissioned. It is intended that the unit will process around 2000 samples each year and, in addition, carry out a limited programme of research. In the first place, this research will be aimed at reducing the size of sample required, as a number of would-be users are currently prevented from making use of the technique simply because they cannot provide sufficient material. A small steering committee chaired by Dr Janet Sprent of Dundee University has been formed to assess applications for analyses and to oversee the running of the unit.

S E Allen

RESEARCH AND DEVELOPMENT

Sunday Telegraph magazine feature

The Sunday Telegraph approached ITE about a feature article they were planning for their colour magazine section, entitled *The quality of life*. The purpose of the article was to examine 7 locations to provide a spectrum of human environments which could be encountered in Britain. ITE was asked to provide technical and scientific help to obtain and interpret environmental data which might be relevant in a survey of this kind.

The sites chosed for the study were:

1. Centre Point, London – a busy traffic junction
2. Bournemouth – a service industry area
3. Moelfre, Anglesey – a rural, maritime area
4. Bradford – an industrial site
5. Norton Disney, Lincs – an arable area
6. Cambridge – leafy suburbia

7. Inverey, Grampian Region – a reputedly 'clean' area

The environmental factors examined included air quality, water quality (rain, mains supply and surface), vegetation, radioactivity and noise. In addition, samples of road and ledge dust were taken and a crude examination of oak trees for type and amount of lichen cover was carried out. The survey covered a period of 3 weeks in winter, and involved a visit to each site. From so few samples it was to be expected that any conclusions would be rather tentative, especially if the inter-site differences were small. However, the results could be expected to portray conditions at each site on the particular sampling day.

The main findings can be summarized as follows.

1. The air quality results were predictable. At 2 of the sites, Bradford and London, the SO_2 concentrations were in excess of 100 μ m^{-3}, whilst Bournemouth was the cleanest urban site. Of the rural sites, Norton Disney was the dirtiest, probably because of the proximity of the Trent Valley power stations and the dust associated with arable farming.

2. The lead content of Bradford rainwater was an order of magnitude higher than the rest. Unfortunately, the London rainwater was contaminated because of nearby building operations during the collection period, and the results were disregarded. The marine influence was apparent at the coastal sites.

3. Tap water analyses showed differences in hardness, and London's water was highest in dissolved salts. The highest level of nitrate-nitrogen was found in the Cambridge sample, and not at Norton Disney as had been expected, probably because of the high fertilizer nitrate application over the water catchment area.

4. Lead levels in vegetation reflected the exposure to vehicle exhaust fumes, and all samples were affected to some extent.

5. The lowest and highest radioactivity measurements differed by a factor of 2, with Inverey in the granite area of Scotland being the highest.

6. The dust samples showed differences in composition between urban and rural areas, the former being characterized by the large amounts of fibres and glass particles.

7. The differences between sites were highlighted by the lichen examinations. It is well known that most species of lichen are sensitive to environmental pollution and the survey lichens correlated well with the quality data in both quantity and number of species present.

J A Parkinson

Freeze concentrator

Research into the variation in soil organic matter under differing tree species required the concentration of aqueous soil extracts prior to their examination by Sephadex gel-filtration and nuclear magnetic resonance spectroscopy. To minimize the effects of temperature change on the extracts and to enable rapid water reduction, a freeze concentrating apparatus was constructed (Plate 40).

A small refrigeration unit freezes pure water on to the sides of a sample bowl, and a stirring paddle wipes the forming ice to prevent entrapment of the solute. A novel method of shutting down the refrigeration when the desired concentration has been achieved is incorporated into the apparatus. The paddle is lifted by the forming ice until the shaft interrupts an infra-red beam. The optical sensor also detects trapping of the paddle by the ice. The refrigeration system switches off within a few seconds of these conditions being sensed.

The method has 2 main advantages over freeze-drying techniques. The solute does not freeze and water is removed from the extract quickly and with minimal attention.

D G Benham

Rain acidity monitor

For studies on the acidity of rainfall, an instrument has been designed and built in collaboration with the University of Wales Institute of Science and Technology to measure and record the pH of rain. The monitor in this instrument measures pH at the time of the rain event, so overcoming some of the problems associated with the collection and storage of samples at a remote site. Of particular importance is the ability of the monitor to follow changes in pH throughout a rain event.

Rain intercepted by an 8 inch rain gauge funnel is collected in a tipping bucket. The bucket tips after each 0·5 mm rain and initiates the measuring sequence. The flow of rain sample through the conductivity and pH measuring cells is controlled by solenoid valves. Once a day the system is automatically checked using a standard buffer solution, followed by thorough washing of the pH electrode. The glass electrode is designed for measuring pH in low conductivity waters. The acidity, conductivity, temperature and timing of each 0·5 mm rain are measured and recorded by a microprocessor-based controller and logger, which enables data for up to 250 mm rain to be recorded in the solid-state memory. A portable microcomputer is used to interrogate the logger and transfer the recorded data back to the laboratory.

G H Owen and C R Rafarel

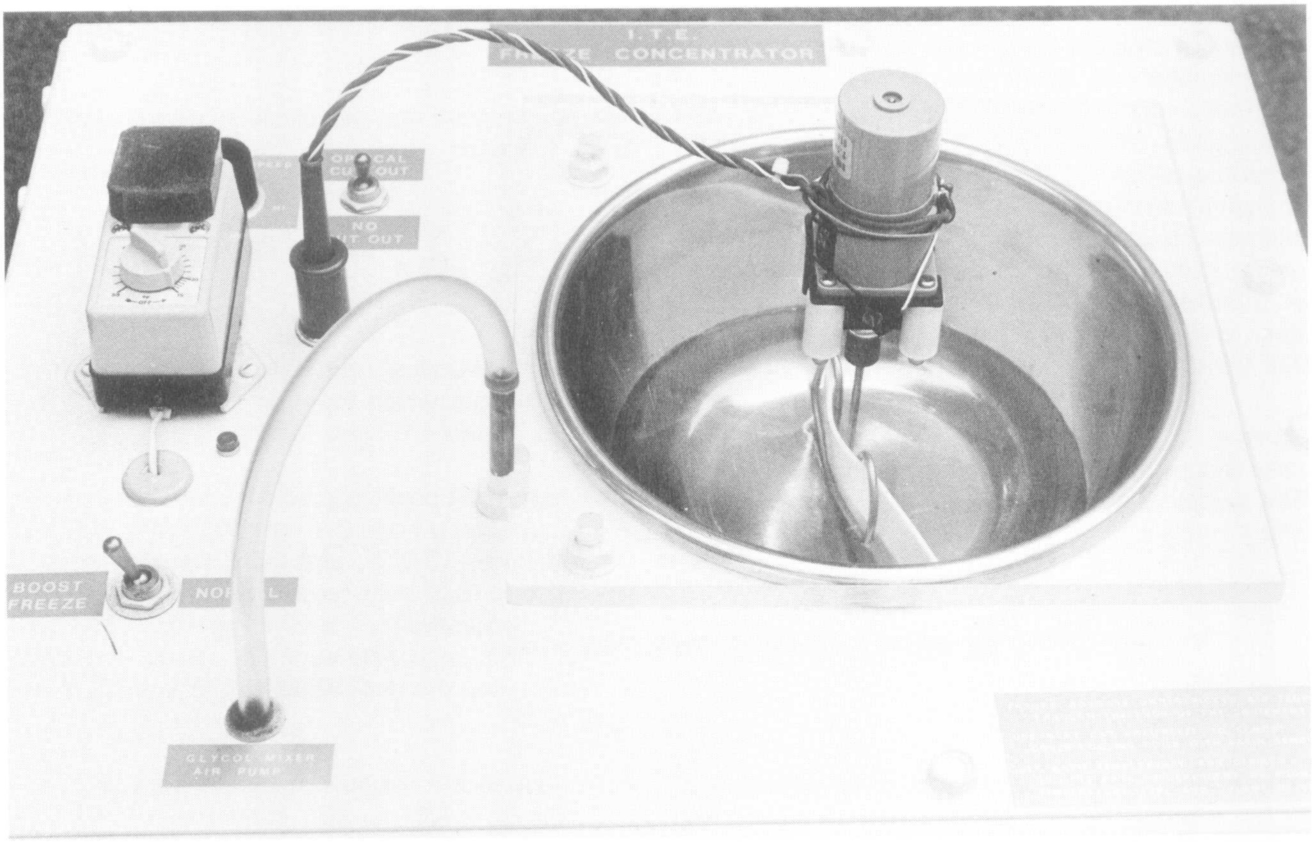

Plate 40 Freeze concentration equipment for the rapid removal of water from labile soil extracts (Photograph D G Benham)

Rainfall trigger unit

In studies on the water chemistry of catchment areas following heavy rain, it is desirable to use stream sampling equipment which can be activated just before the initial flushing occurs. Equipment was constructed, including a tipping bucket collector which increments a counter after each 0·5 mm rain. When a pre-set count is reached, a trigger signal is generated to activate the external sampling equipment. In addition, an internally generated pulse also decreases the counter response which, in time, delays the count due to rainfall. Consequently, an isolated rainfall event not large enough to exceed the trigger level will then have no effect on subsequent rain events.

The unit was designed using low-power circuitry and is housed inside the cover of a commercially available rain gauge. The trigger level and decay rate can be set by thumb-wheel switches.

C R Rafarel

Programme 15
SYSTEMS ANALYSIS AND BIOMETRICS

TWO-DIMENSIONAL SPECTRAL ANALYSIS OF SPATIAL PATTERNS IN VEGETATION

The structure of vegetation is determined by a range of biological mechanisms and environmental influences which can result in distinctive spatial patterns. However, whilst the existence of spatial pattern can frequently be detected as a departure from random, its accurate description, sufficient to permit inference about the mechanisms which have produced it, is difficult. For this task, a description of pattern must have generality, ie the analytical technique used should not limit the type of pattern which can be described.

Two-dimensional spectral analysis provides this generality through a comprehensive description of both the structure of pattern, including the presence of directional components, and its various scales. It is a general interrogative technique and assumes no structural characteristics in the data prior to analysis. Two main functions are used (Renshaw & Ford 1984).

1. The spatial autocorrelation matrix (C_{jk}/s^2) estimates their successive neighbours.
2. The periodogram (I_{pq}) shows the extent to which the data contain periodicities at different frequencies.

The structure of a forest canopy

The canopy structure of a 39-year-old thinned commercial plantation of Scots pine (*Pinus sylvestris*) at Thetford Forest, UK, containing 1000 trees ha^{-1} was investigated. An area 36 m × 120 m was surveyed. Horizontal extent of the individual tree crowns was measured along parallel transects spaced at 1 m intervals. Height and location of each tree, and crown height at its perimeter were measured; crown height at intermediate distances between perimeter and trunk was estimated by geometric projection (Figure 93i) (Ford 1976).

X_{st} ($s = 1,...,m$; $t=1,...,n$) is the array of data, in this case canopy heights, after subtracting the mean value. The sample autocovariance at lag (j,k) for $0 \leq j < m$ and $-n < k < n$ is defined by:

$$C_{jk} \sum_{s=1}^{m-j} \left[\sum_{t} (X_{st} X_{s+j,\ t+k}) \right] \quad (1)$$

where the second summation is taken over $t=1,...,n-k$ if $k \geqslant 0$ and over $t=k+1,...,n$ if $k<0$. The spatial autocorrelation matrix is given by (C_{jk}/s^2) where s^2 denotes the sample variance (X_{st}). The full matrix has a central value of $C_{oo}/s^2=1$, ie the data 'correlate perfectly' with themselves, and values at increasing distances from the centre are estimates of the correlation between points and their successively more distant neighbours. Usually, each possible neighbour pair is represented only once, and a matrix of entries almost twice the size of the data matrix is obtained.

The spatial autocorrelation matrix of a 32 × 32 matrix of canopy heights at 1 m spacing exhibits a strong row effect, with an approximately equal phase shift between successive rows, and has the appearance of 2 orthogonal systems of waves (Figure 93). The regularity of features approximately the size of tree crowns indicates that tree crowns have some regularity in shape and in their distance apart. The occurrence of tree crowns grouped together in a wave-like structure was not expected when the survey was made.

A more compact description of spatial pattern than that provided by the spatial autocorrelation matrix is frequently obtained by the periodogram or sample spectral function, and shows the extent to which the data contain periodicities at different frequencies. The data are transformed by cosine waves of different wave-lengths, and, in the analogy of tuning a radio set, entries in the periodogram represent the signal at discrete but small bands of reception. The transformation apportions the sample variance between the range of frequencies. The size of the sample area limits the detection of low frequency, ie large-scale patterns, whilst the number of sample units (m,n) limits the detection of high frequency, ie small-scale patterns.

The periodogram may be calculated via the autocovariance function:

$$I_{pq} = \sum_{j=-m+1}^{m-1} \sum_{k=-n+1}^{n-1} C_{jk} \cos\left\{ 2\pi \left(\frac{jp}{m} + \frac{kq}{n}\right) \right\} \quad (2)$$

Two main features are apparent in the periodogram of canopy heights which together contribute 71·6% of the total variance (Figure 93iii).

I. A ridge in the positive quadrant which has 2 parts. A low frequency ridge (Ia) from position (1,0) to (8,4) contributes 19·07%, and the 2 large elements at (4,1) and (8,2) both have a direction value, Ø, of 76%. Separated from Ia by a single row is a ridge of high frequency elements (Ib) which contributes 6·09%, and the peak value is 1·78% at (12,4) with Ø = 72°.

II. A ridge in the negative quadrant from (4, − 4) to (15,1) (Ø = 135° to 86°) contributes 46·4%. The high frequency elements are mainly clustered between 90° and 95°, and reflect an effect of the planting row. A plot of the number of zeros in each row of the data against row number (1 to 32) clearly showed the presence of 2 cyclic components: a low frequency cycle of wave-length 21 rows and a high frequency oscillation with 11 complete cycles occurring over 25 rows. This latter cycle corresponds to a wave-length of 2·3 m and a frequency of 14·1 which is near the centre of the group of high frequency components. The absence of canopy is clearly of major importance in its effect on spectral structure.

Taken together, ridges I and II strongly suggest the presence of a powerful directional component. They provide evidence for tree crowns being aligned at an angle of 70° to the direction of tree planting, and these rows have a sinusoidal structure with wave-length approximately equal to 8 m. This structure was certainly not apparent when the canopy was viewed above from a meteorological mast.

The spectra of 8 partially overlapping 32 × 32 submatrices of canopy heights ($X^{(r)}d2s_t$) ($r=1,...,8$) was calculated using rows 1-32, 12-43, ..., 78-109. The percentage of variation explained was consistent throughout, and the general features present were similar. However, as r is increased (Figure 94), the most marked difference is a shift in the percentage of variation attributable to the low frequency components: Ia reaches a maximum for r=4, at which point IIa reaches a minimum. The high frequency components are more stable, with IIb showing slight oscillations and Ib a shallow concave shape with a

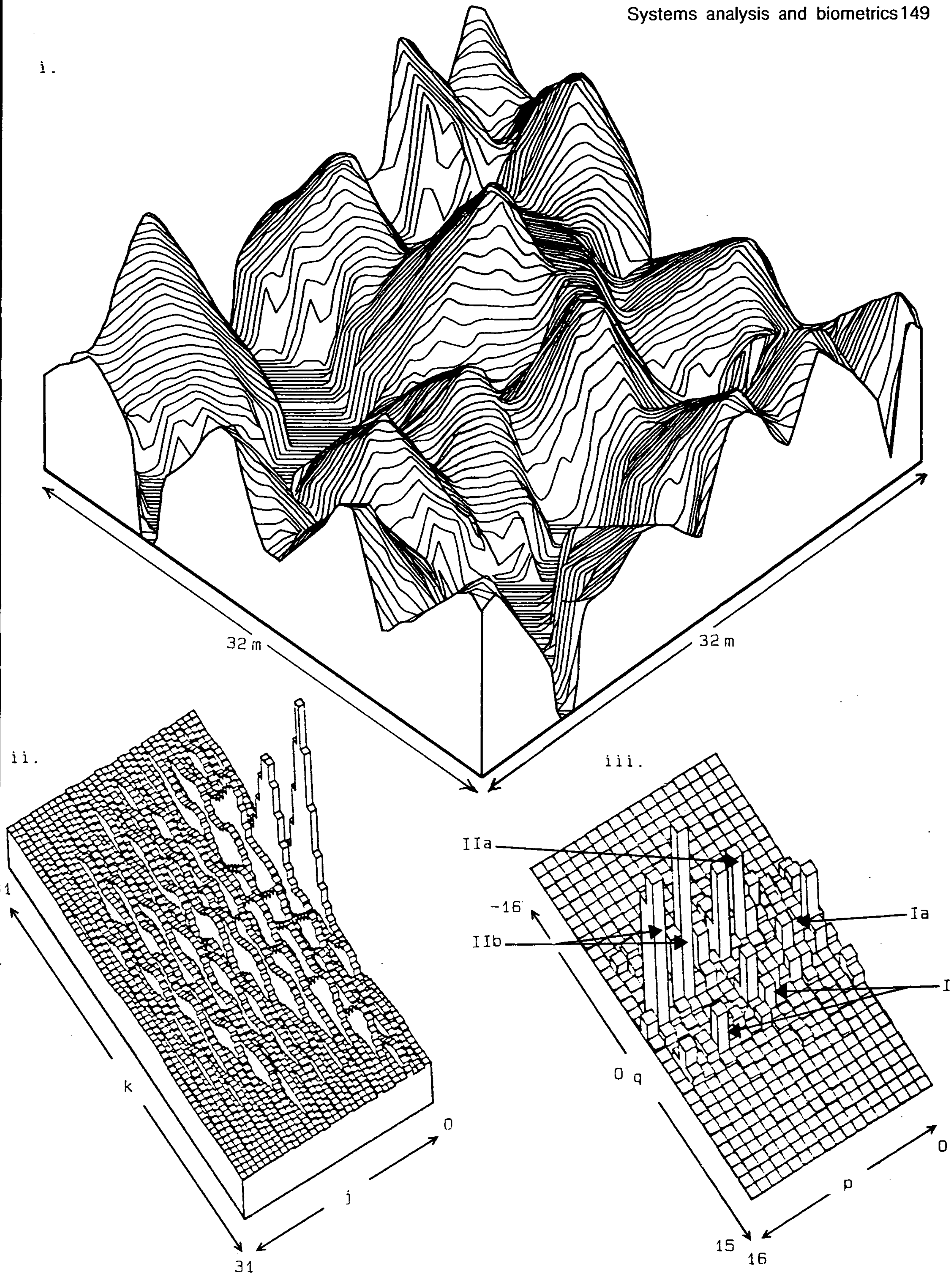

Figure 93 *i. A perspective SYMVU drawing of the surface of a 39-year-old Scots pine plantation at Thetford Forest*

ii. Spatial autocorrelation matrix of a 32 m × 32 m section of the canopy surface; for explanation, see text

iii. The periodogram derived from (ii) with principal features as described in the text labelled and with their percentage contribution to the total variance

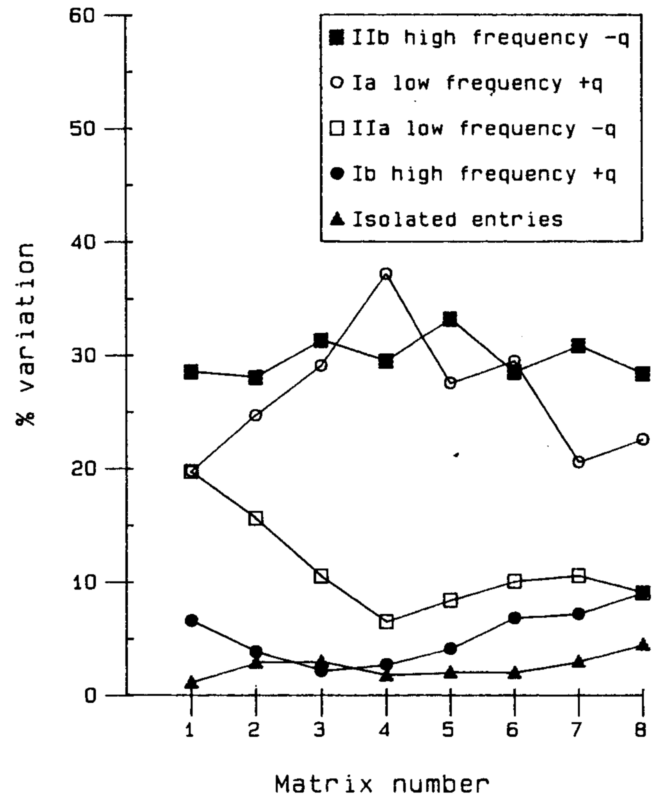

Figure 94 The percentage of variation attributable to different features in the periodograms of successive 32 m × 32 m blocks of forest canopy

minimum at r=3. The contribution of III, the variance due to isolated entries in the spectrum, remains low. These changes in the spectra reflect real changes in the structure of the forest. This site was being used for micro-climatological measurements (Ford 1976), and a large mast together with areas preserved for sensitive instruments was situated in rows 30-60. Two years previous to this canopy survey, a light thinning was made, but subsequent enquiries revealed that there had been a tendency to remove fewer trees around the instrument mast and preserved areas, and the changes in the spectrum across the plot can be interpreted in relation to this difference in thinning. Where there has been less thinning, ie in the centre of the plot, the wave-like aggregation of tree crowns is strongest. The effect of planting rows, feature IIb, remains virtually unaltered throughout.

These features in the pattern of the forest canopy are related to (i) competition between trees; (ii) directional growth of tree crowns, which has a major effect on the structure of the canopy not appreciated before the survey was made; and (iii) differences in management which, though small and not apparent during the survey, nevertheless influence structure. Renshaw and Ford (1983) present a detailed analysis and assessment of statistical significance.

Two-dimensional spectral analysis has been made of both the numbers of plants of rosebay willowherb (*Epilobium angustifolium*), spreading in a woodland following the thinning of trees, and also of the cover of heather (*Calluna vulgaris*) in a regenerating Scots pine forest (Ford & Renshaw 1984). In both cases, the spectral analysis showed that the distribution of plants was the result of more than one ecological process. The spectra of simulation models were used in the interpretation.

*E D Ford and E Renshaw**

(*University of Edinburgh)

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THE RELATIONSHIP BETWEEN SHOOT WATER POTENTIAL AND TRANSPIRATION RATE IN SITKA SPRUCE

The cell water potential of shoots could be a useful indicator of the health of Sitka spruce (*Picea sitchensis*) growing in managed plantations. The commonest way of estimating water potential requires the removal of a shoot for measurement in a 'pressure bomb'. This destructive method is particularly labour intensive if data on changes of water status under varying weather conditions are required. Techniques are now available to measure automatically the trans-

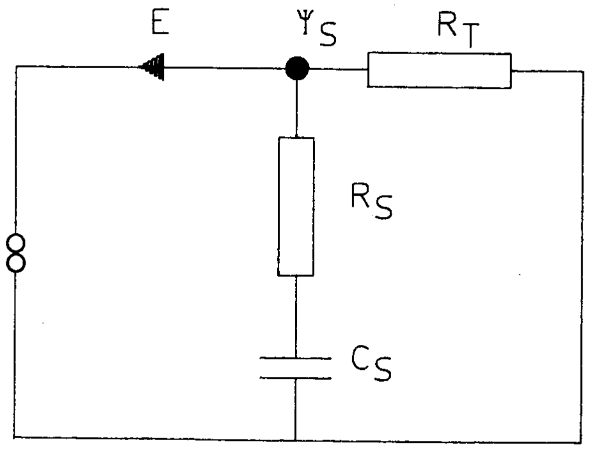

Figure 95 Resistance capacitance network for water movement in Sitka spruce

E	*transpiration flow*
ψ_3	*shoot water potential*
R_S	*resistance to water flow from trunk storage*
C_S	*capacitance of trunk storage*
R_T	*resistance to flow along trunk*

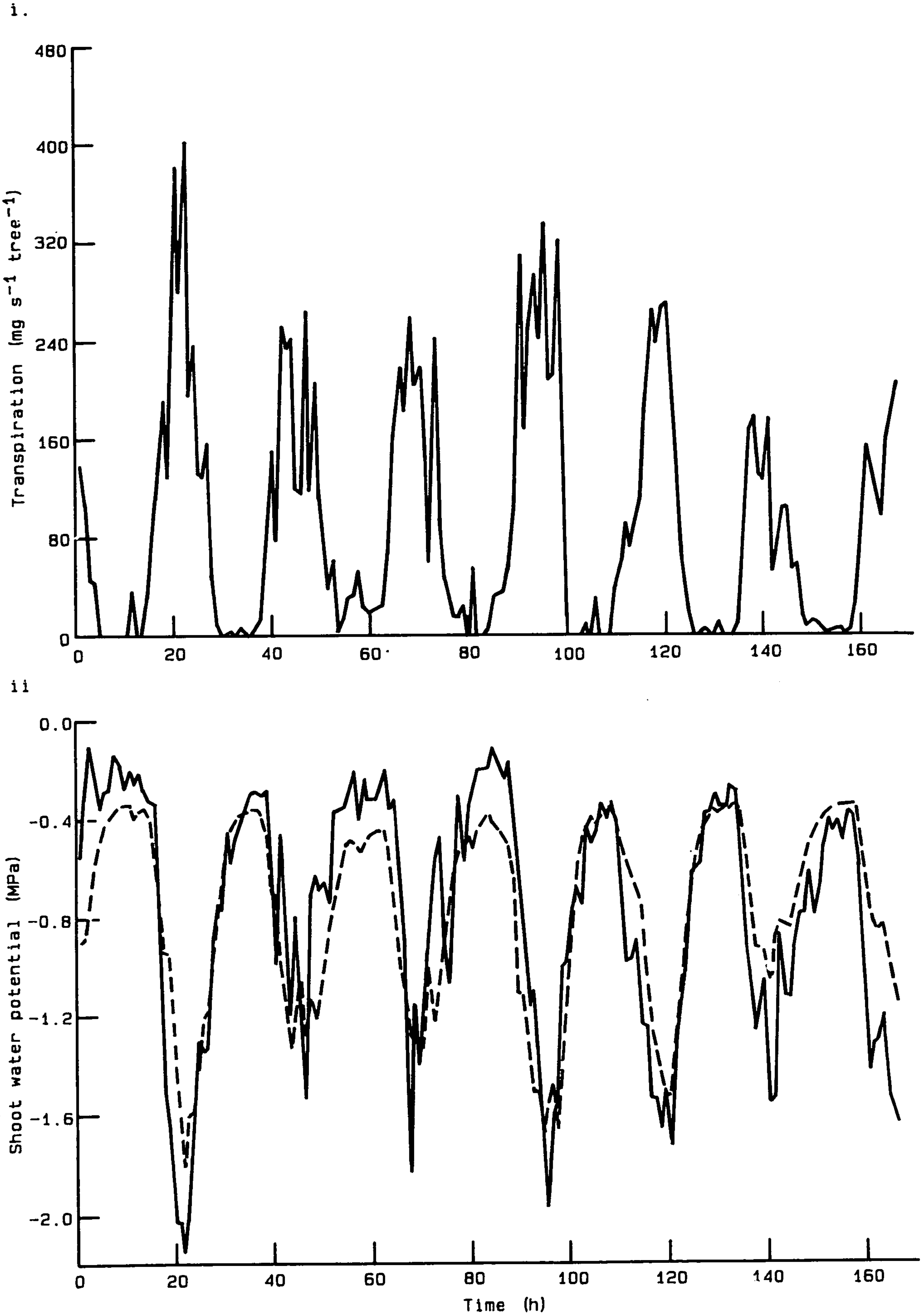

Figure 96 *Hourly measurements of transpiration rate and water potential (——) in shoots at whorl 13 with model for water potential from first order discrete-difference equation (– – –) for Sitka spruce, 14 years old, in Greskine Forest, south-west Scotland*

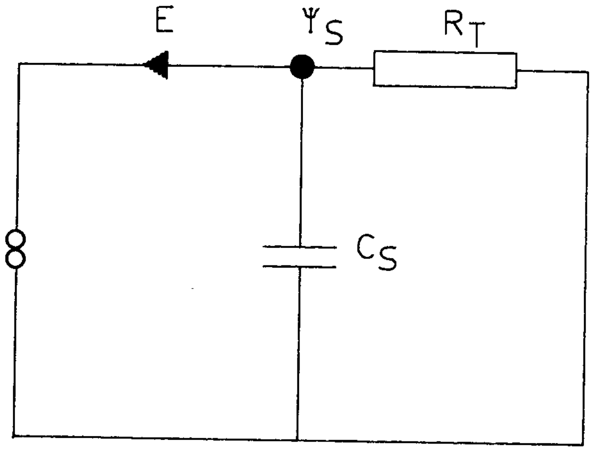

Figure 97 Resistance capacitance network for water movement in Sitka spruce equivalent to fitted first order discrete-difference equation

piration rate of a forest, and, as well as being in themselves interesting, such measurements might be able to be used to predict resultant changes in shoot water potential. Milne and Young (1985) have described 2 models relating shoot water potential in Sitka spruce to transpiration rate. The first model is the resistance-capacitance analogue of Milne *et al.* (1983) (Figure 95). The more interesting second model uses a discrete-difference equation which, although less mechanistic than the above, is of simpler structure.

Data consisting of 168 consecutive hourly measurements of transpiration rate and shoot water potential were recorded in July-August for a 14-year-old Sitka spruce plantation at Greskine Forest, south-west Scotland (Figure 96). Transpiration was measured using the eddy correlation/energy balance technique and the water potential of shoots on the 13th whorl from the ground was measured by a Scholander-type pressure bomb (Milne *et al.* 1983).

The first order discrete-difference equation:

$$\psi_t + a_1\psi_{t-1} = b_o E_t$$

where ψ_t is shoot water potential and E_t is the transpiration rate at time t, was fitted to the data. The fitting was carried out on a microcomputer, using a

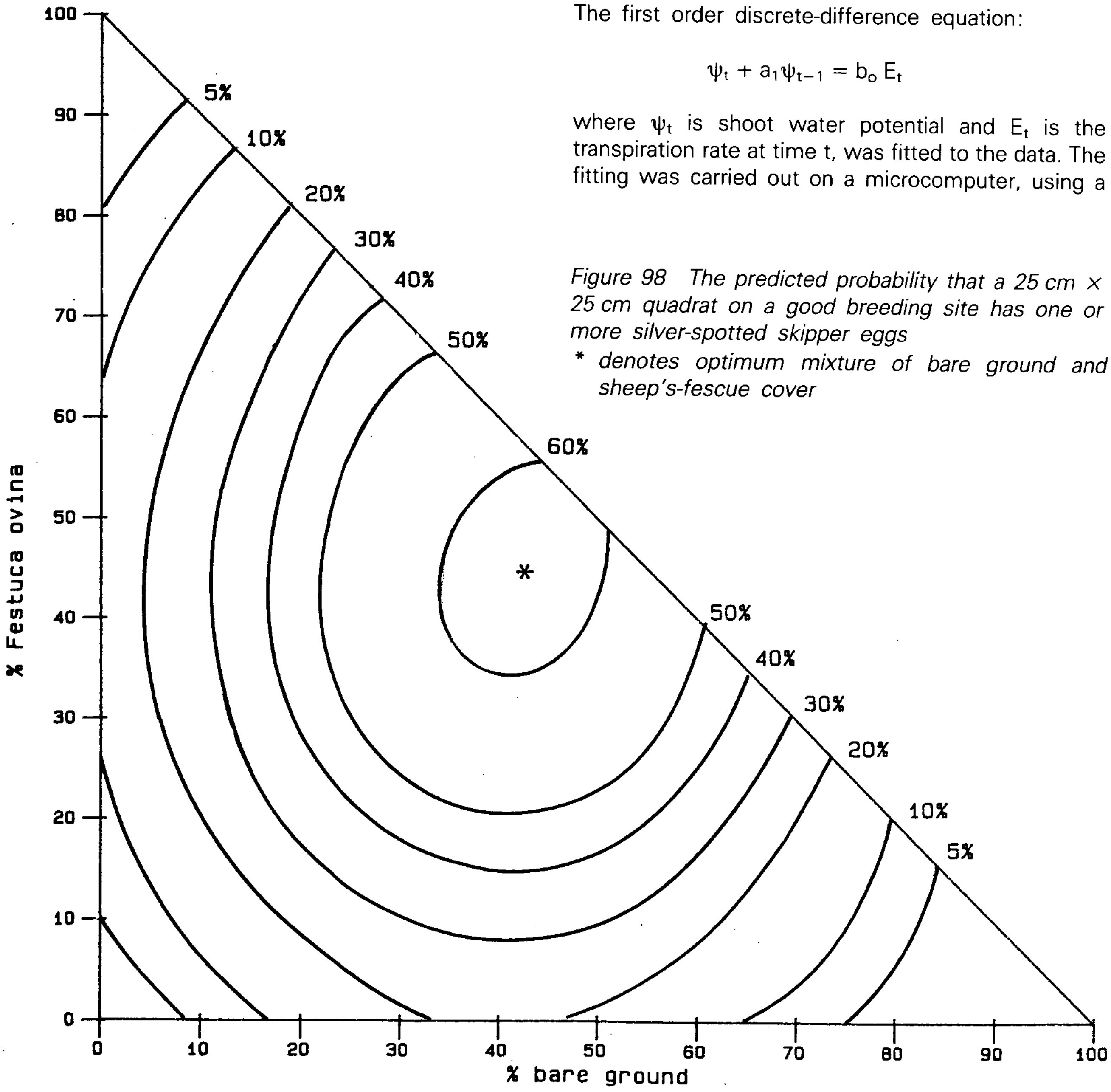

Figure 98 The predicted probability that a 25 cm × 25 cm quadrat on a good breeding site has one or more silver-spotted skipper eggs

- ** denotes optimum mixture of bare ground and sheep's-fescue cover* programme developed by Young (1984). His work on the use of a recursive solution of an instrumental-variable method to replace the matrix optimization methods of Box and Jenkins (1970) for discrete-difference equations has allowed these analyses to be executed simply and quickly, without recourse to a mainframe computer.

The first order model was selected from other possible orders by a quantitative identification procedure based on the coefficient of determination and error variance norm (Young *et al.* 1980). The first order model had a single autoregressive parameter (a_I) of value $-0{\cdot}63$ and a single moving average parameter (b_o) of $-0{\cdot}0019$. The coefficient of determination was 0·69 and the water potentials estimated by the model are shown in Figure 96. Under some simple assumptions, a first order discrete-difference model can be taken as equivalent, in analogue terms, to a resistance and capacitance in parallel (Figure 97), the trunk resistance in this case having a value of $5{\cdot}03 \times 10^{-3}$ MPa mg^{-1} s^{-1} and the storage capacitance $1{\cdot}55 \times 10^{6}$ mg MPa^{-1} (Milne & Young 1985).

The fit of the model to the data is encouraging and could be useful in practical situations. Recent work using an extension to the instrumental-variable methods to allow for time variation in the parameters suggests this to be the source of remaining error, rather than a lack of complexity in the model.

R Milne
(in co-operation with Professor P C Young, Department of Environmental Sciences, University of Lancaster)

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ESTIMATING THE OPTIMUM MIXTURE OF SHEEP'S-FESCUE COVER AND BARE GROUND FOR EGGS OF THE SILVER-SPOTTED SKIPPER

The silver-spotted skipper (*Hesperia comma*) is restricted to calcareous grassland where its larvae feed on sheep's-fescue (*Festuca ovina*) (Heath *et al.* 1984). It is a declining species in Britain, and its current status of about 50 populations is causing grave concern among conservationists. One worrying aspect of the decline was that there was no obvious cause: many population extinctions had occurred on sites (including some Nature Reserves) that still contained an abundance of sheep's-fescue. It was suspected that the micro-structure of the grassland might be as important for successful breeding as the abundance of the food-plant. This suspicion was strengthened when it was found that females deposited their eggs mainly on small fescues. The research described below aims to give practical guidelines on the optimum percentage 'cover' of both bare ground and fescue within each patch of micro-habitat on a site.

The percentage cover of bare ground (%B) and sheep's-fescue (%F), and the presence or absence of eggs of the silver-spotted skipper were recorded for each of 281 25 cm × 25 cm quadrats on a good breeding site on the North Downs in Surrey.

The probability (P) that a quadrat had one or more eggs was described by the following logistic model (all terms statistically significant ($P<0{\cdot}01$)):

$$\begin{aligned}\text{logit}(P) = \log_e\,(P/(1-P)) = -3{\cdot}711 + 0{\cdot}115\,(\%B) - 0{\cdot}00141\,(\%B)^2 \\ + 0{\cdot}0832\,(\%F) - 0{\cdot}000913\,(\%F)^2\end{aligned}$$

Logit(P) is a meaningful scale on which to model P because it gives a simple way of expressing how the quantitative effect of the degree of bare ground (%B) varies with the percentage cover of sheep's-fescue (%F), and *vice versa*. The model is fitted by maximizing the likelihood of the observed egg distribution.

Figure 98 shows the predicted probability of eggs occurring in a 25 cm × 25 cm patch for all combinations of bare ground and sheep's-fescue cover. The optimum mixture for egg deposition (and presumably egg and larval survival) is about 40% bare ground and 45% fescue cover, within each small patch of around 25 cm × 25 cm. During the past 30 years, many traditional breeding sites have become overgrown, with both sheep's-fescue and other plants increasing at the expense of bare ground. It is possible that this increase has been responsible for most population extinctions, as eggs are rarely deposited where there is little bare ground and dense swards of sheep's-fescue (Figure 98).

Among surviving populations, adult densities and the predicted suitability of each site for egg laying (based on the model above) were reasonably correlated ($r=0{\cdot}75$). Thus, the optimum cover combination for which any site manager should aim will be the same as in Figure 98, although obviously the actual probability of finding eggs will depend on the history and size of the site, its degree of isolation from other populations, and the weather.

R T Clarke and J A Thomas

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CROSS-IMPACT MODELLING

The technique of modelling complex inter-relationships between variables is now well established in a wide variety of scientific disciplines. Such models represent formal expressions of the essential elements of a problem in either physical or mathematical terms. In ecology, for example, models can be used to express the flow of energy through the various compartments of an ecosystem, or the succession of different vegetation components in time. In sociology and economics, models are widely used to illustrate and predict the changes taking place in human systems with development and resource depletion. Such models are especially useful when the relationships between the many essential variables are complex, non-linear or display what the engineer calls 'feedback' - the carrying back of some of the effects of a process to a previous state so as to strengthen or modify it. Because it is usually easier to experiment with the model than with the real system that it represents, modelling provides opportunities for the decision-maker to test his theories before committing them to real-life application.

Almost all of the real problems of the everyday world involve large numbers of competing variables, and present a complexity of behaviour that taxes the human capacity for comprehension. As a result, most day-to-day decisions are made in a space which is truncated by reducing the number of variables that are considered in the solution of the problem. Simulation models tend to be excessively numerical, concentrating attention on those variables which can be readily quantified, and excluding variables which, while important, are basically subjective in nature. It was for this reason that Kane (1972) sought to develop a simulation procedure by which technically unsophisticated users could quickly become fluent in the logical expression of cross-impact relationships.

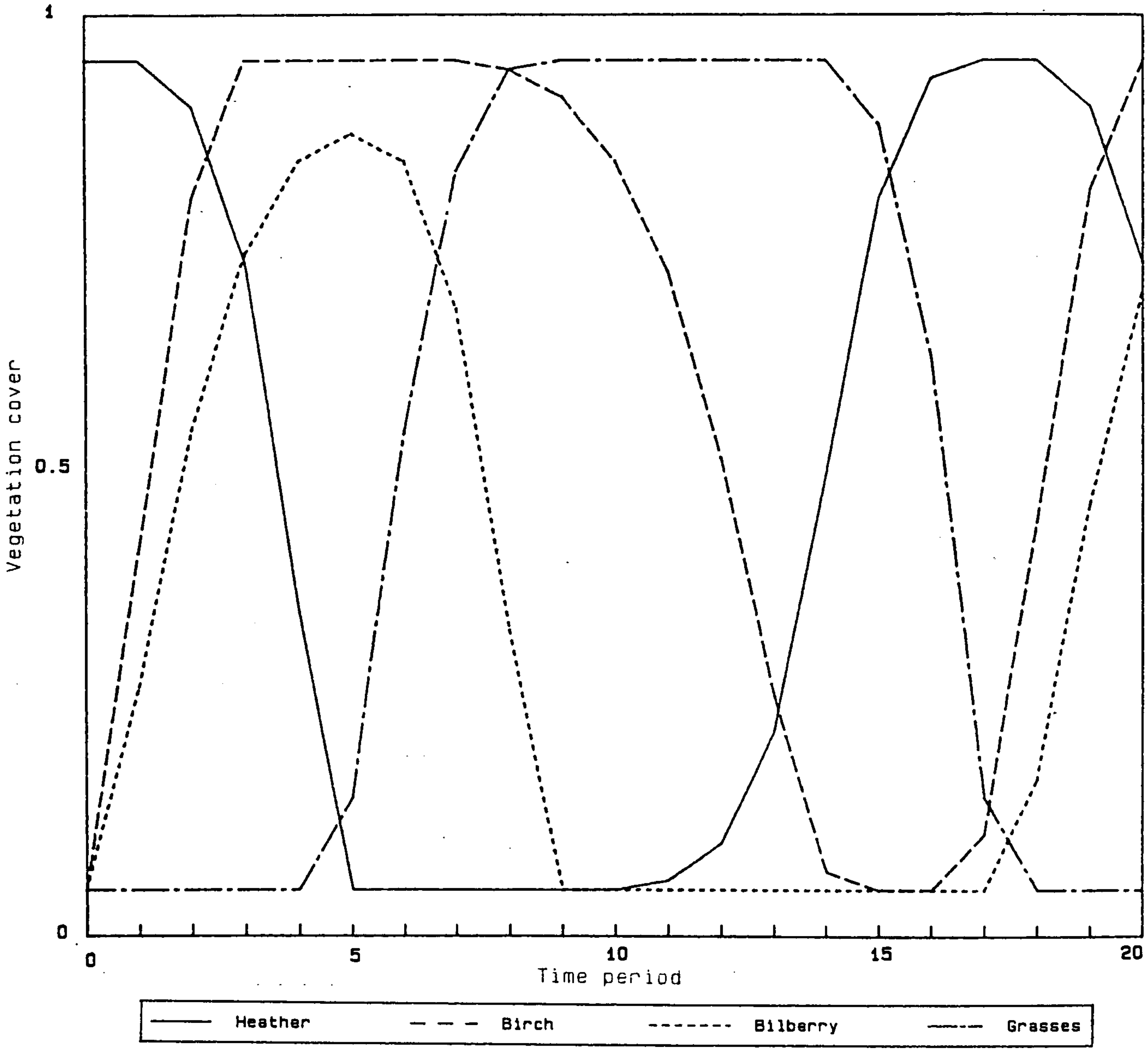

Figure 99 Cyclic changes in vegetation succession on moorland invaded by birch

The method of cross-impact modelling permits the investigation of the relationships between several (perhaps many) variables, some of which may be subjective, in the sense that they cannot necessarily be measured accurately on an objectively defined scale. To accomplish this investigation, the modeller assesses the degree of impact between sets of paired variables, and then allows the cross-impact algorithm to calculate the successive states of the variables as they change over time or space. If the changes in the successive states are reviewed, preferably graphically, the modeller obtains an improved perception of how the variables in the system interact, and thus gains an understanding of how the hypothetical system behaves. Of course, he still has to establish that the model is a fair representation of the real system, through direct experimentation. An added advantage of this kind of modelling is that it can often be used to develop efficient experimental tests of the adequacy of the model.

Cross-impact models are therefore primarily concerned with structure and form, rather than with very precise numerical specifications. While remaining unambiguous, they are implicit in that they tend to reflect verbal or mental images, and are best used as aids to learning or communication. Because they are most often concerned with policy and strategy, they tend to be future-orientated. As a result, they may be utilized by persons interested in policy decisions, who have to consider major structural changes rather than small changes in an existing system. The computations are easily programmed for a computer, and the ability to work interactively on the modern microprocessor makes cross-impact modelling a powerful and exciting way of exploring the behaviour of hypothetical systems. The simplicity of the model formulation allows alternative ideas to be explored in a self-consistent fashion. The modeller is given a free choice in the design of the model, without being burdened by mathematical or computational complexities. He is also free to change his conception of the structure of the system as his intuition into its behaviour improves.

A further advantage in the use of the modern microprocessor lies in the access provided by such machines to fast and interactive graphics. The successively calculated values of the system variables, when plotted on to a simple graph, give a rapid insight into the behaviour of the system. Each change made to the formulation of the system provides a new graph which can be compared with those already drawn. Graphs can be recalled or replotted at will, and the user of such a modelling system easily recognizes that he or she is in complete command of the system, with nothing to get between the mental models of how the system behaves and the actual behaviour of the system as it is defined.

Figure 99 shows the output from a cross-impact model of vegetation succession on moorlands, with the suppression of the heather (*Calluna vulgaris*) by birch (*Betula* spp.) and bilberry (*Vaccinium myrtillus*). The birch woodland is, in turn, invaded by grasses which prevent the regeneration of the birch, thus enabling the heather to re-invade and initiate a new cycle of successional states. This figure, interestingly, is almost exactly the same as that given by Miles (1981) to describe the generalized sequence of vegetation changes occurring during the life cycle of a birchwood.

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References

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CULTURE CENTRE OF ALGAE AND PROTOZOA

GENERAL REPORT

Last year's Report (Baker 1984) referred to the abolition of the practice of charging a reduced rate for cultures supplied to educational establishments in the UK. In the first 2 months following this abolition, sales of cultures fell by 80%; during the remainder of the year, the number sold has remained almost exactly at this level, when compared to the previous year. Between 1 September 1982 and 31 August 1983, 3656 cultures were sold, 3248 of them (89%) at the reduced rate. For the succeeding 12 months (1 September 1983 to 31 August 1984), the total was 748, with 441 (59%) going to organizations which would previously have been charged the lower rate. This year's total is thus 20·5% of the previous year's total, while sales to UK schools and colleges have dropped to 13·6%. It is interesting that, as a result of the increase in the full rate charged, the estimated gross income from sales has risen slightly - from about £12,800 in 1982-83 to about £13,700 in 1983-84.

Work is continuing on up-grading the collection. The curators (Mrs E A Leeson, N C Pennick and J P Cann) are critically examining the holdings, discarding uncharacterized material of no possible interest, and, where necessary, actively seeking to acquire strains of potential scientific or biotechnological value. Several strains of the alga *Dunaliella* have recently been obtained. Nearly 50% of the 2000 or so strains in the collection are now axenic; about 300 are protozoa, many of which cannot be axenic as they require other organisms as food.

The transfer of the ITE Administrative Headquarters to Monks Wood resulted in the moving to CCAP of one of the biometricians, D F Spalding, who is continuing with the computerization of the Centre's bibliographic data and strain records.

Much of the Centre's research work is described elsewhere in this Report (G J Morris *et al.*, pp 80-82; R A Gardner, pp 125-126; J R Baker & P Cox, pp 124-125). Routine cryopreservation has been proceeding by the study on the effects of long-term preservation on the viability and stability of micro-organisms, being undertaken for the Department of Trade and Industry (DTI). However, the impending arrival of Miss Karen Jackson, a 'sandwich' student from the North-East London Polytechnic, in January 1985, to work for 6 months with Dr G J Morris on the cryopreservation of algae, should enable this work to be extended. A co-operative cryopreservation project with the Scottish Marine Biological Association is planned.

Other continuing collaborative projects include those with the British Antarctic Survey (K J Clarke: feeding mechanisms of krill), the Institute of Cytology in Leningrad (F C Page: taxonomic characters of amoebae; G J Morris and Mrs G C Coulson: cryobiology of amoebae), the University of Salford (R A Gardner: parasites of bats), the Marine Biological Association of the UK (J R Baker: trypanosomes of cartilaginous fish), Coralab Research Ltd (K J Clarke: electron microscopy; J R Baker: trypanosomal antigens) and ITE's Monks Wood and Furzebrook stations (J R Baker: parasites of squirrels).

Long-term visiting workers at the Centre this year have been Professor J O Kessler (a Fulbright Fellow from the University of Arizona, also visiting the University of Cambridge Department of Applied Mathematics and Theoretical Physics) and Dr R L Blanton (University of Georgia, USA). Other visitors, for shorter periods of study, included Dr C F Bardell (University of Tuebingen), Dr J Sikora (Nencki Institute, Poland) and Dr H R Preisig (University of Zurich) - a welcome regularly returning migrant.

About 15 delegates to the third meeting of the European Culture Collections Curators' Organization, held in Norwich, spent a day at the Centre on 20 July.

J R Baker

Reference

Baker, J. R. 1984. Culture Centre of Algae and Protozoa. *Annu. Rep. Inst. terr. Ecol. 1983,* 197-109.