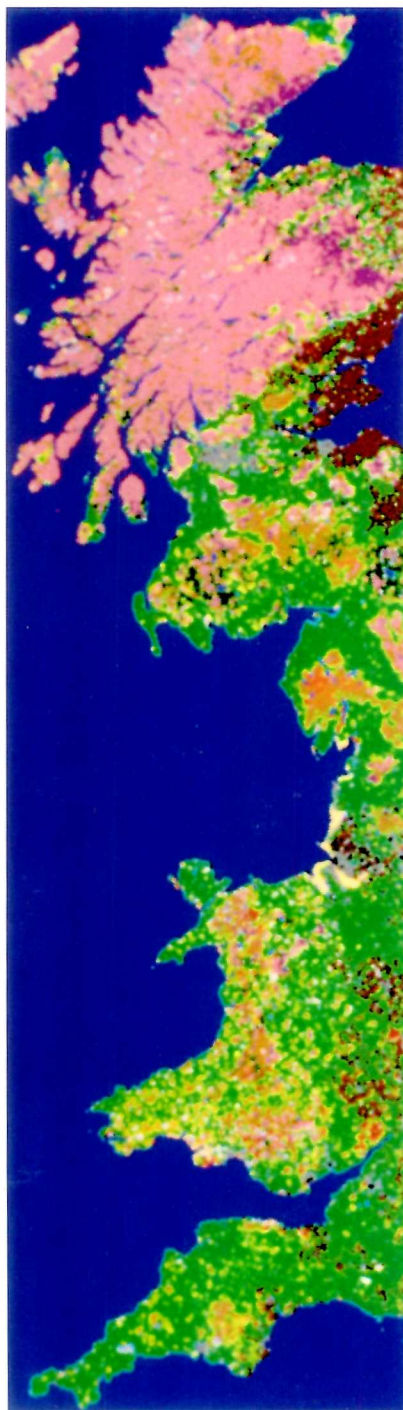


1992 — 1993
R E P O R T



**Institute of
Terrestrial
Ecology**

Natural Environment Research Council

The ITE mission

The Institute of Terrestrial Ecology will develop long-term, multidisciplinary research and exploit new technology (molecular ecology, information technology, and modelling) to understand the science of the natural environment, with particular emphasis on terrestrial ecosystems

Priority is placed on developing and applying knowledge in the following areas

- the factors which determine the *composition, structure, and processes* of terrestrial ecosystems, and the *characteristics* of individual plant and animal species
- the dynamics of *interactions* between atmospheric processes, terrestrial ecosystems, soil properties and surface water quality
- the development of a sound scientific basis for *modelling and predicting* environmental trends arising from natural and man-made change
- the *dissemination* of this research to decision-makers, particularly those responsible for environmental protection, conservation, and the sustainable use of natural resources

The Institute will provide training of the highest quality, attract commissioned projects, and contribute to international programmes

By these means, ITE will seek to increase scientific knowledge and skills in terrestrial ecology, and contribute to national prosperity and prestige

Front cover illustration

An overview of the ITE land cover map of Great Britain

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**Report of the
Institute of Terrestrial Ecology
1992–93**

Natural Environment Research Council

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Population and community ecology

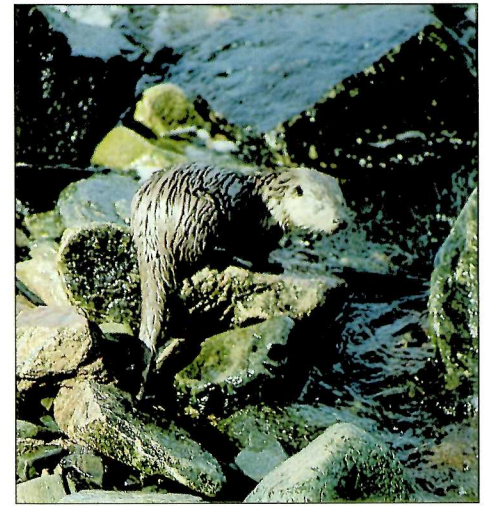
This Programme investigates the factors and processes that determine the distribution and abundance of populations of single-species and of communities of species populations, at different spatial scales. It includes the study of plant/herbivore, predator/prey, host/parasite and competitor interactions. In studies of single-species populations, much attention is also given to genetic, physiological and behavioural aspects. The main applied applications of the work lie in the fields of conservation, pest control and impact assessment. The present Programme was formed in 1993 by combining the two former Programmes 8 and 9, which were concerned with population biology and community ecology, respectively. This merger arose because investigating populations in isolation of the community to which they belong, and investigating communities without reference to the properties of their constituent species populations provide only a partial understanding of the processes involved at each level.

At present, projects and subprojects are concentrated in ITE South, where there

are 15 projects (56 subprojects), compared with ITE North's four projects (28 subprojects). In addition to these projects based in five ITE research stations, the Programme contains:

- i. the recently established NERC Special Topic programme on Wildlife Diseases, with projects being undertaken in several establishments, but led from ITE Monks Wood;
- ii. the Integrated Screening Programme, based at the University of Sheffield;
- iii. the Unit of Behavioural Ecology, based at the University of Oxford;
- iv. the Centre for Population Biology, based at Imperial College at Silwood Park.

The Programme contains many projects of high scientific quality as well as contributing directly to strategic research of both potential and immediate practical value, as the following reports illustrate. The first two, on the populations of a shorebird and plant that inhabit the intertidal zone of estuaries, use quite



different modelling approaches to make predictions about the entirely new environmental conditions created by, for example, sea level rise associated with global warming or building barrages for electricity generation. The next report illustrates how research helps to identify when there is a genuine conflict between alternative uses to which natural resources can be put, in this case freshwater fish stocks and their conservationally significant osprey predators. The next article shows experimentally how red deer browse Sitka spruce trees according to their size and shape; there is no evidence that either fertilizing or shading trees affected their use by deer by changing the nature of the chemical defence compounds the trees deposit in their shoots. Using very different organisms and geographical scales, the next three reports illustrate the increasingly recognised requirement to understand the effects of the spatial configuration of our fragmented countryside on the organisms that depend on it. The first describes how the distribution pattern of vegetation influences the use that sheep and, to a lesser extent, deer make of it. The next asks what an individual animal must do, in this case the tawny owl, when the suitable fragments of habitat become smaller than its home range requirements. The third considers the colonisation of patches of straw by fungi, simultaneously evaluating current theoretical models of habitat fragmentation, while contributing to our understanding of interactions that are important in maintaining the fertility of the soil. The last article illustrates the application of community ecology to applied problems, by reporting an experiment in which an entire community of vegetation was translocated from one site to another, an ambitious option for habitat restoration that has rarely been attempted.



Plate 34. An otter: one of the many species studied by scientists within this Programme

J D Goss-Custard

Modelling the effect of winter habitat loss on shorebird populations

Each summer and autumn, many hundreds of thousands of shorebirds arrive from their summer breeding grounds to forage on the estuaries and coastal flats of Britain (Plate 35). Many remain for the winter, but a significant proportion move on to wintering areas further south, having first replenished their fat reserves to fuel the sometimes enormous distances involved. During their annual cycle, shorebirds thus depend on resources that span almost every latitude of the globe, from the breeding areas as far north as the Arctic, down to wintering areas as far south as southern Africa.

British estuaries, like others in north-west Europe, are mainly used on passage or by overwintering birds. The birds feed on the small number of dominant macro-invertebrate species that frequently occur in enormous densities, especially in the organically rich fine sediments. Because of the open nature of the terrain and resulting scarcity of shelter from winds, shorebirds have particularly high energy demands. In cold and windy weather, many may die: their elevated energy demands are difficult to meet because their cold, and so inactive, prey are difficult to locate. Accordingly, conservationists are concerned that the many human activities that occur on estuaries might make it even more difficult for shorebirds to find sufficient food, either to fuel their return migration

to the breeding grounds in spring or simply to survive the winter. Accordingly, the UK government has signed a number of international agreements, committing the country to provide protection for the globally significant populations of these specialised coastal birds.

The activities that might impinge on shorebirds are numerous, ranging from the small-scale, such as dog-walking and casual shellfishing, to large-scale developments for recreational, commercial or agricultural purposes. The effect of many of these activities is to prevent the shorebirds from using intertidal food supplies that they would otherwise exploit. The question is whether or not the displaced shorebirds would be able to re-establish themselves successfully on the mudflats and sandflats that remain elsewhere. For example, ITE was asked to predict whether the nationally significant numbers of redshank (*Tringa totanus*) and dunlin (*Calidris alpina*) that feed in Cardiff Bay could be supported by the intertidal flats of the adjacent Severn Estuary if the Bay were to be converted into a freshwater lake. The answer will vary from place to place according to the scale of shore loss involved and its quality as a feeding area. There is, therefore, a need to predict when a proposed activity will affect shorebirds and when it will not.

Such predictions are required at several scales. At one extreme, only local predictions are required, as when we are asked to anticipate the effects on

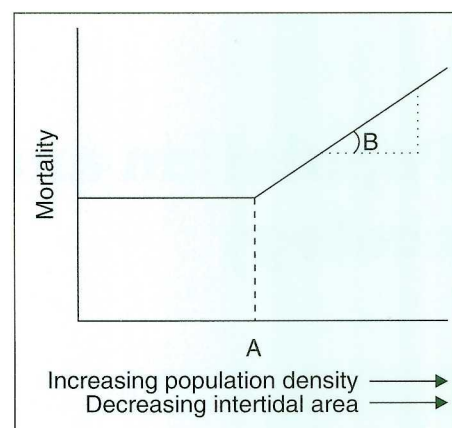


Figure 50. How the mortality rate of overwintering shorebirds may change as the density of birds on estuaries increases. The slope B measures the strength of the density-dependent mortality that starts when the population density has reached A

local bird numbers of a narrowing of the shore through land reclamation. At the other extreme, a prediction may be required of the effect of sea level rise, for example, on the size of a species population across its entire range. These are challenging scientific questions; making predictions for such new circumstances tests our basic understanding of the systems we investigate. How ITE is developing models to make predictions at the local scale was discussed in a recent Annual Report (Yates & Jones 1992). This article briefly summarises how we aim to make predictions at the continental scale, using an approach detailed by Goss-Custard and Durell (1990) and Goss-Custard (1993).

The effect of winter habitat loss on global population size will depend on the extent to which competition for food between birds will be intensified by the same numbers of shorebirds being forced to feed together at higher densities in the reduced area that remains. This competition, in turn, depends on the strength of the feedback loop that links bird density to the rate at which individual birds can feed, and thus their chances of surviving the winter and leaving for the breeding areas in good condition. ITE has been studying these feedback processes for a number of years, and is constructing a series of models that will enable us to predict better how habitat loss would affect shorebird numbers.

The effect of these feedback processes on winter mortality rate is illustrated in Figure 50, which shows how the



Plate 35. An individually colour-ringed oystercatcher foraging on an estuarine bed of mussels

proportion of birds failing to obtain enough food might change with population size. At low population sizes, there is little competition between birds, most individuals can feed in the best areas and few are affected by interference from other birds or from the food supply being depleted over the winter. Some birds die, but their death is unrelated to density. However, as numbers increase, competition intensifies until a point A is reached at which birds begin to die because they cannot compete. Mortality then becomes 'density dependent' and increases at rate B for every unit increase in bird density, B more individuals die. The greater the value of B, the stronger is the density-dependent mortality acting on the population in winter.

For practical reasons, the values of A and B are very difficult to measure in wild populations of shorebirds. Yet their values are critical for determining how the population size will respond to habitat loss in winter. Figure 51 illustrates how the population size of one species, the oystercatcher (*Haematopus ostralegus*), is affected by the removal of an increasing proportion of its winter feeding habitat, assuming different values of B, the value of A is kept constant throughout. The many other parameters of the model are based on a synthesis of the data from population studies conducted over 40 years. These data include the clutch size, and the hatching and fledging success of

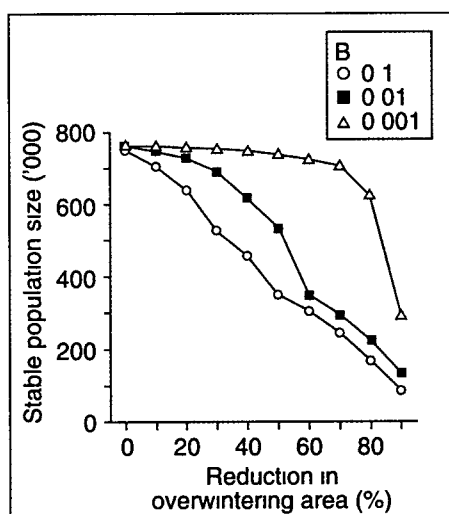


Figure 51 The effect on the overall population size of reducing the wintering habitat of European oystercatchers by up to 95%, as shown by modelling. The effect varies according to the value of B, the strength of the density-dependent mortality occurring in the winter.

oystercatchers in different parts of their summer range. They also include competition for breeding territories, which determines how many birds breed and introduces a strong source of density dependence in the summer. However, as Figure 51 shows, the strength of the winter density-dependent mortality, as measured by B, has an important effect on how the entire population will be affected by winter habitat loss, even though regulation also occurs on the breeding grounds in the summer.

We, therefore, need to estimate the quantity of B if reliable predictions are to be obtained. This estimation is being done in a long-term study of oystercatchers wintering on the Exe Estuary in south Devon. The approach is illustrated in Figure 52. The quality of the food supply of oystercatchers, like that of other shorebirds, varies from place to place. As bird numbers increase, competition causes birds to spread over the 'food gradient', so that an increasing proportion feed in the poorer areas. As a result, as well as the intensifying competition that also occurs in even the high-quality areas, an increasing proportion of birds fail to feed well enough to avoid starvation. The proportion dying at any one population size will depend on the variation that occurs in the habitat and amongst the birds themselves. Thus, the greater the proportion of the available feeding habitat that is of good quality, the higher the population size will be before density-dependent mortality sets in. Similarly, the greater the variation between birds in their susceptibility to interference from other birds, the sooner density-dependent mortality will begin as bird numbers increase, and the lower will be the rate of increase with bird density.

We are now able to make a provisional estimate of B from our field studies over 15 years on the variation that occurs amongst mussel beds and oystercatchers on the Exe. An empirical model has been built to predict on which mussel bed individuals of specified foraging and competitive ability feed at different population sizes. In this game theory model, each individual decides where it is best for it to feed, in the light of the decisions taken by all the other birds in the population on where they should feed. The rate at which a particular bird feeds depends on its own foraging efficiency, on the quality of the mussel

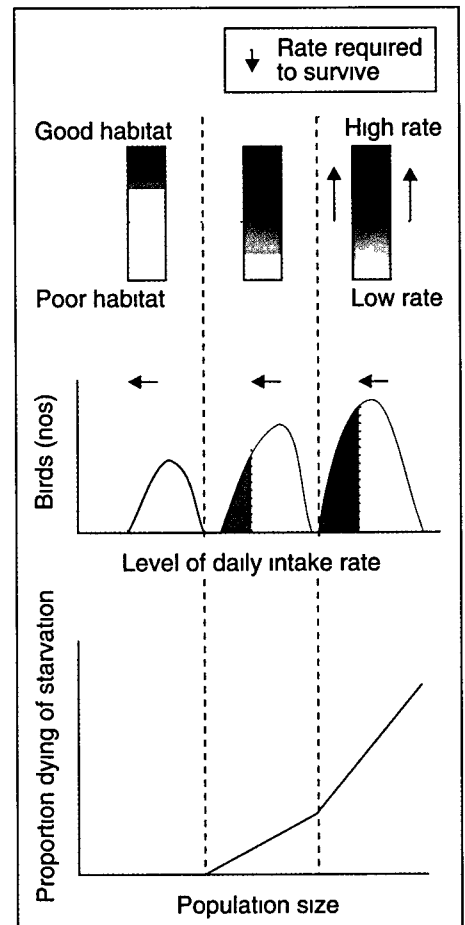


Figure 52 How investigating the way in which a population of individuals becomes distributed over their variable food supply allows the proportion dying to be predicted. In the game theory model of this process constructed for oystercatchers feeding on mussels on the Exe Estuary, most of the parameters have been measured empirically in the field.

bed, and on the severity of the competition from other oystercatchers. This rate, in turn, depends on the bird's competitive ability relative to those of the other birds on the same bed. When the model is run, each individual is moved, in random order, to what is currently the most rewarding mussel bed for that bird. After a series of such iterations, when the distribution of birds has stabilised, the proportion failing to achieve the intake rate required to survive is calculated, giving a prediction of the overwinter mortality rate. The model is then rerun with a different population size, allowing mortality to be predicted at another population density. Being based on extensive and long-term field studies of the variations in the many habitat and bird variables involved, the model should provide a reasonable estimate of the strength of the winter density-dependent mortality.

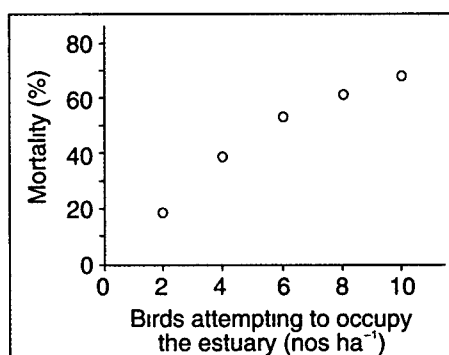


Figure 53 The proportion of oystercatchers dying of starvation at different population densities, as predicted by the game theory distribution model

The first, and thus provisional, output of the model is given in Figure 53, which suggests that the value of A , where mortality becomes density dependent, is about one bird per ha of intertidal mudflat. This value is just below the average density of oystercatchers on British intertidal flats in winter, suggesting density dependence might occur at the present population size of oystercatchers in Britain. Mortality increases with density at the approximate rate (B) of 0.07 per one bird per ha increase in bird density. As Figure 51 shows, this value implies that gradual winter habitat loss could lead to a gradual decrease in total population size, even though quite strong regulation also occurs in the summer.

This work represents the first attempt to estimate the strength of the critically important density-dependent function from studies of the behaviour of individual birds. Undoubtedly, the precise values of the quantities A and B for oystercatchers will be refined as further simulation and empirical work proceeds. For example, there is a need to define more precisely the many parameters involved, especially those relating to habitat and individual variation. Under a contract from the Joint Nature Conservation Committee, we are now also exploring ways of estimating B over a large number of estuaries, by including the risks and costs associated with birds migrating each autumn and spring and moving between estuaries in winter. There is also a need to review published estimates of all the parameters used in the model to generalise the findings on the particularly well-studied oystercatcher to other species. The results so far are encouraging and illustrate how very important population parameters, such as B , can be derived

from behavioural studies of individual birds. Being based on fundamental properties of the birds' behaviour, it is hoped that such studies will provide a sounder basis for predicting for wholly new circumstances than is presently available. By addressing *post hoc* why the numbers of some species have declined, much conservation science has been reactive. The work described here aims to develop a predictive conservation science for an important group of birds which will allow us to anticipate with some confidence what would happen were a particular policy to be implemented or event to occur.

J D Goss-Custard, R T Clarke, R W G Caldow and S E A Durell

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A niche model of *Spartina anglica*

(This work was funded by the Energy Technology Support Unit, Harwell, under its tidal energy research and development programme)

The prospect of changes in tidal conditions around the world's coastlines presents a major challenge to estuarine ecologists. In addition to rising relative sea levels, acute changes in tidal regime created by man-made structures, such as estuarine barrages, are likely to have a fundamental impact on intertidal organisms (Gray 1992a). Predicting the direction and magnitude of this impact depends on understanding and quantifying those aspects of the tidal regime that control the distribution and size of plant and animal populations and, where possible, generating predictive models based on these aspects.

The factors which control the distribution of saltmarsh plants are believed to be predominantly tide-related and, in particular, to reflect the interaction between variations in tidal submergence and in various biotic and edaphic factors. The pattern, frequency and depth of tidal submergence at a given point in a saltmarsh are determined by local surface elevation. The range of elevations over which a particular species may be found, ie its vertical range, can be regarded as its elevational or tidal niche – a niche which in broad terms has lower limits imposed by increasing tidal submergence and upper limits imposed by competition with other species (Pielou & Routledge 1976, Davey & Costa 1992, Gray 1992b). A recent study funded by the Energy Technology Support Unit has provided the opportunity to measure the elevational range of several saltmarsh species and to produce and parameterise a simple niche model for predicting species' distributions in novel situations. Initial effort has concentrated on the invasive and frequently dominant species at the lowest elevations, the grass *Spartina anglica*.

The upper and lower limits of *Spartina* were measured along 107 line transects across saltmarshes in 19 estuaries in south and west Britain, from Poole Harbour on the south coast to Morecambe Bay in the north. Some transect data were taken from earlier studies and from the literature, but most were from a field survey in 1988. Nearby Ordnance Survey benchmarks were to be used to obtain heights of the upper and lower limits in metres above Ordnance Datum (OD), and for each transect a total of 31 variables was recorded. These included variables recorded from maps (such as 'estuary area', 'fetch in the direction of the transect', and 'latitude') and from tide tables (such as 'range of spring tides', 'mean high water springs' and 'mean high water neaps'), as well as those recorded in the field (such as 'length of transect' and 'sediment type'). Variables derived from the primary data were also calculated – these included 'estuariness' (the distance of the transect from the upstream tidal limit expressed as a proportion of the total distance between the upstream tidal limit and the estuary mouth), as well as various measures of tidal submergence, such as 'percentage of tide-free days' and 'maximum number of consecutive submergences', both on an annual basis and at selected stages of the growing season.

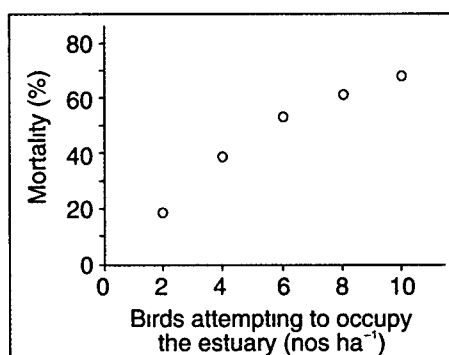


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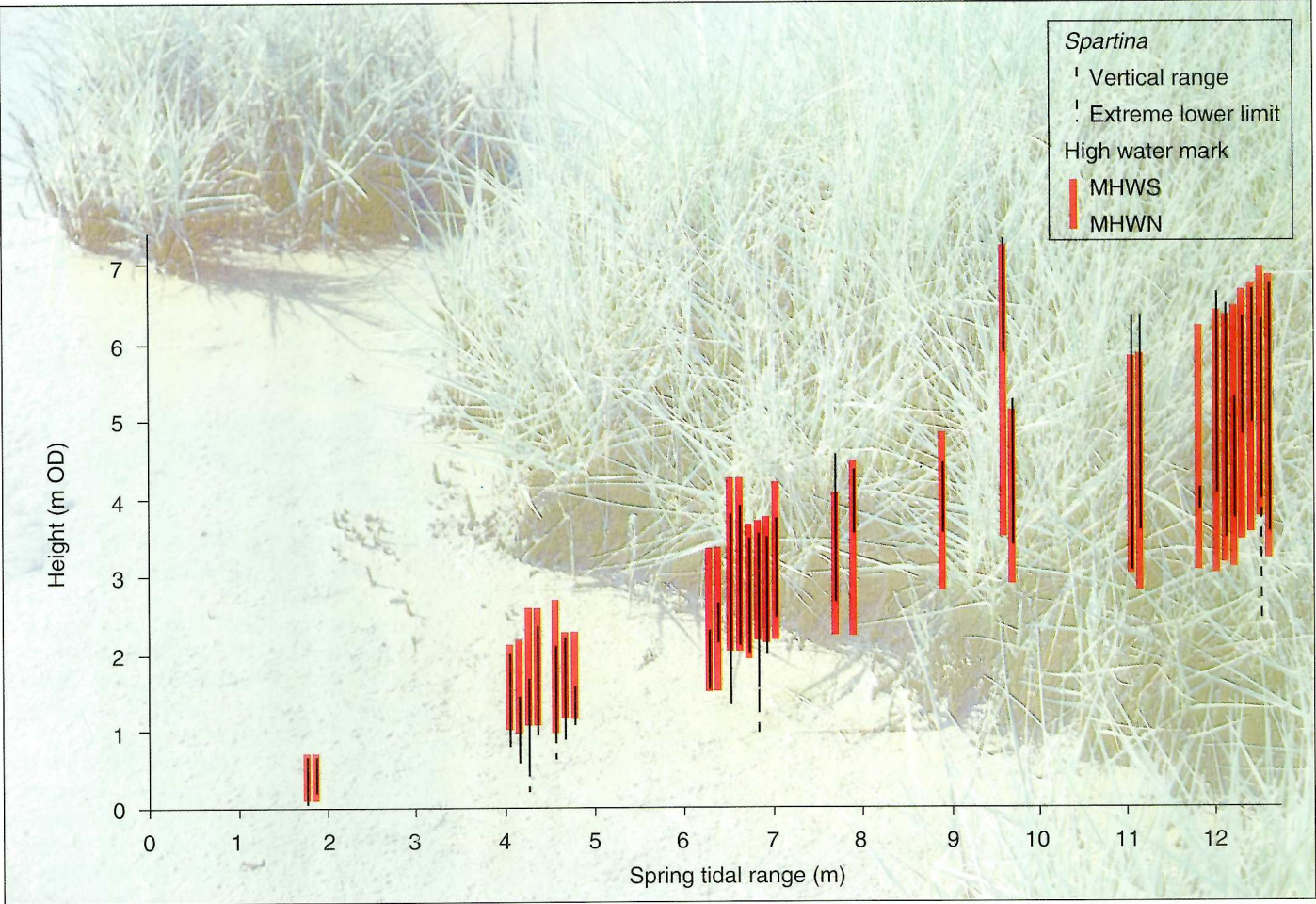


Figure 54. Vertical range of *Spartina anglica* marsh and spring tidal range for 32 sites from 20 estuaries. From left to right: Poole Harbour (2 lines), Foryd Bay, Teign, Dovey, Mawddach, Traeth bach, Tamar, Tavy, Milford Haven (2), Tywi, Taf, Red Wharf Bay, Conwy, Lavan Sands, Loughor, Dee, Ribble, Mersey, Shepperdine, Morecambe Bay, Severn (10 sites)

The properties of the data matrix of 107 transects and 31 variables were explored using the statistical package MINITAB. Initial examination of the full correlation matrix was followed by the development of a multiple regression model.

A striking feature of the data was the relationship between the vertical range of *Spartina* and tidal range, as indicated by the range of mean spring tides. Figure 54 shows that, in general terms, *Spartina* occurs between the mean high water neap (MHWN) tide level and the mean high water spring (MHWS) tide level, and that it extends below MHWN in estuaries of smaller tidal range (less than 7 m) and extends above MHWS in areas of large tidal range (more than 7 m). As one might expect, the upper and lower limits of the species are closely related to tidal range. Simple linear regression against spring tide range gives:

$$LL = -0.826 + 0.451 (\text{RANGE ST}) \quad R^2=86.1\% \quad S=0.52$$

(0.127) (0.018)

and

$$UL = -0.571 + 0.528 (\text{RANGE ST}) \quad R^2=88.7\% \quad S=0.54$$

(0.132) (0.018)

where LL and UL are the lower and upper limits of *Spartina* along each transect (in m OD Newlyn); R^2 is the percentage of variation in the limit accounted for; and S is the residual standard deviation in *Spartina* limit (in m). (The figures below the equation in brackets are the standard errors.)

Although an extremely high proportion of the variation in limits (86–88%) is accounted for by variation in tidal range alone, it was found that other factors had an effect, and that the addition of other variables to the regression equation significantly improved its fit, as measured by the increase in R^2 . The additional effect of each variable was considered in turn and eventually a 'best' equation was produced for each limit.

$$LL = -0.805 + 0.366 (\text{RANGE ST}) \quad R^2=88.7\% \quad S=0.54$$

(0.13) (0.019)

$$+ 0.053 (\text{FET TRAN}) + 0.13 (\text{EST AREA})$$

(0.016) (0.025)

$$- 2.14 (\text{BEACHLEY}) \quad R^2=93.7\% \quad S=0.35$$

(0.264)

and

$$UL = 4.74 + 0.483 (\text{RANGE ST}) \quad R^2=90.2\% \quad S=0.50$$

(2.29) (0.028)

$$+ 0.068 (\text{FET TRAN}) - 0.099 (\text{LATITUDE})$$

(0.020) (0.045)

where FET TRAN is the fetch in the direction of the transect (measured in km up to a maximum of 10 km); EST AREA is the surface area of the estuary expressed as $\log_e$ area (km^2); LATITUDE is latitude in degrees from north (expressed as a decimal); and BEACHLEY is a dummy variable added to allow for two outlier transects at Beachley in the Severn Estuary on which *Spartina* extended downshore by around 2 m more than predicted from the tidal range equation (for reasons which are unknown but are not believed to be due to levelling errors).

The ability to account for more than 90% of the variation in the elevational limits of the plant is remarkable. A prediction of this unheard-of precision in a biological model suggests that special factors may be operating. These factors are likely to include the fact that, as the occupant of the lowermost zone, *Spartina*'s distribution is likely to be dominated by physical factors, rather than biotic interactions.

The variables measuring fetch and estuary area both have positive effects, pushing the limits further up the shore, and presumably reflect the effects of increasing wind-generated wave and current strengths on more exposed mudflats and in larger estuaries. The physical effects of tidal submergence are known to be important in regulating the establishment of saltmarsh plants. Latitude has a negative effect: in more northerly marshes, the upper limit of *Spartina* is found further downshore. This may be a reflection of the species' relative inability to compete with other species, particularly *Puccinellia maritima*, in shorter growing seasons and at lower spring temperatures. *Spartina* is one of only eight species in Britain which utilise the C4 photosynthetic pathway, a method of photosynthesis which is commoner in tropical plants and is less efficient at low temperatures.

The utility of the equations describing the vertical limits of *Spartina* lies mainly in their provision of a model which predicts the potential area that the plant may occupy in an estuary it has yet to invade. It may also predict the species' response to other changes, such as those induced by rising sea levels or by the construction of coastal barriers or defences. In particular, such a predictive model may be used to gauge the effects of tidal energy barrages on saltmarshes, especially in those parts of the estuary where tidal range or fetch is changed. In those areas upstream of a barrage where the water is held before discharge through the turbines at low tide, the change in tidal regime with a prolonged high water stand involves the loss of the sinusoidal tide curve. In order to improve predictions of the effect of this type of change, it will be necessary to develop niche models which tease out from the tidal range model those aspects of submergence which are most important in controlling the plants' distribution. Such models are currently

being developed for *Spartina* and a range of other species.

A J Gray, R T Clarke and E A Warman

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Osprey predation on a simple fish community

The populations of many large vertebrate predators are thought to be food-limited under some specific conditions, but the mechanisms by which food limits populations are often unclear. Furthermore, predation may play a considerable part in constraining the growth of prey populations and in shaping their communities. Predator/prey models have been developed to include factors such as the age structure and sex ratios of the interacting populations, resource limitations and the patchy distribution of prey populations, and a choice of alternative prey species. Models help in identifying the major processes which determine the dynamics of interacting populations, though many are based on scant field evidence.

ITE is currently engaged in a major field study in the Muir of Dinnet National Nature Reserve, north-east Scotland, a complex mosaic of aquatic and wetland habitats dominated by two relatively large lochs: Lochs Davan (42 ha) and Kinord (82 ha) are approximately 800 m apart and have an average depth of 1.2 m and 1.5 m, respectively. The lochs

contain populations of eel (*Anguilla anguilla*), perch (*Perca fluviatilis*) and pike (*Esox lucius*) and considerable numbers of their predators, including otters (*Lutra lutra*), mink (*Mustela vison*), osprey (*Pandion haliaetus*), goosander (*Mergus merganser*) and grey heron (*Ardea cinerea*). Perch and pike are themselves predatory and are also subject to sport fishing by man. The project aims to quantify the relationships between three parameters:

- i. predator distribution and foraging ecology;
- ii. fish densities and productivity; and
- iii. the food resources of the fish populations.

It also involves the experimental removal of certain parts of the fish population.

One of the main relationships within the food web under investigation is that between ospreys and their prey. Studies involve the effects of weather on osprey foraging, and the role of osprey predation in the population dynamics of pike and perch. The pike is a common top predator of freshwater ecosystems in Europe and North America, and is often found in association with perch. Such simple fish communities are relatively common in Scotland where the geographical ranges of both species have been extended by man. Sport fishing for pike is increasingly popular in Scotland, but it has a significant effect on the size composition of pike populations; as bigger fish are removed, large numbers of smaller ones predominate. The effects of such changes on the numbers and dispersion of piscivorous predators are unknown. Because the conservation and management of ospreys are of national and international importance, the results of the present study are relevant to similar ecosystems elsewhere.



Plate 36. To obtain an unbiased catch, electrofishing was carried out within a net enclosure

The ability to account for more than 90% of the variation in the elevational limits of the plant is remarkable. A prediction of this unheard-of precision in a biological model suggests that special factors may be operating. These factors are likely to include the fact that, as the occupant of the lowermost zone, *Spartina*'s distribution is likely to be dominated by physical factors, rather than biotic interactions.

The variables measuring fetch and estuary area both have positive effects, pushing the limits further up the shore, and presumably reflect the effects of increasing wind-generated wave and current strengths on more exposed mudflats and in larger estuaries. The physical effects of tidal submergence are known to be important in regulating the establishment of saltmarsh plants. Latitude has a negative effect: in more northerly marshes, the upper limit of *Spartina* is found further downshore. This may be a reflection of the species' relative inability to compete with other species, particularly *Puccinellia maritima*, in shorter growing seasons and at lower spring temperatures. *Spartina* is one of only eight species in Britain which utilise the C4 photosynthetic pathway, a method of photosynthesis which is commoner in tropical plants and is less efficient at low temperatures.

The utility of the equations describing the vertical limits of *Spartina* lies mainly in their provision of a model which predicts the potential area that the plant may occupy in an estuary it has yet to invade. It may also predict the species' response to other changes, such as those induced by rising sea levels or by the construction of coastal barriers or defences. In particular, such a predictive model may be used to gauge the effects of tidal energy barrages on saltmarshes, especially in those parts of the estuary where tidal range or fetch is changed. In those areas upstream of a barrage where the water is held before discharge through the turbines at low tide, the change in tidal regime with a prolonged high water stand involves the loss of the sinusoidal tide curve. In order to improve predictions of the effect of this type of change, it will be necessary to develop niche models which tease out from the tidal range model those aspects of submergence which are most important in controlling the plants' distribution. Such models are currently

being developed for *Spartina* and a range of other species.

A J Gray, R T Clarke and E A Warman

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Plate 36. To obtain an unbiased catch, electrofishing was carried out within a net enclosure



Plate 37. Keybones (jaws and opercula bones) were used to identify and estimate the size of osprey prey items

The decline and subsequent recovery of the Scottish osprey population are well documented; there are currently about 100 breeding pairs. Despite the rapid population growth and intensive study at a small number of nest sites, little is known about the foraging ecology of the species in Scotland. For instance, it is not known whether the birds select fish of particular species or size. Ospreys recolonised the Dinnet study area in the early 1980s, when details of their prey were collected by two local amateur birdwatchers, K Duncan and I MacLeod. Since recolonisation, predation by ospreys could have influenced the population dynamics of this simple perch/pike community.

Pike and perch populations were assessed in both study lochs between

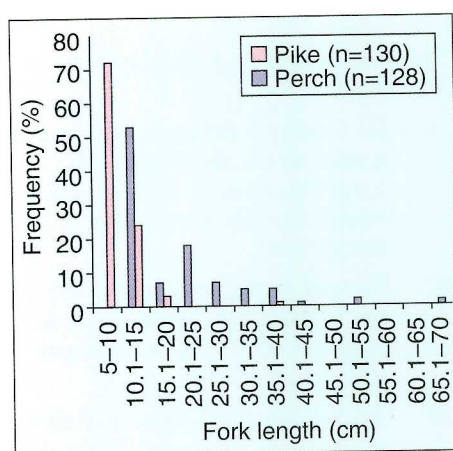


Figure 55. The length frequencies of pike and perch caught by electrofishing

May and September 1990–92 by electrofishing (Plate 36). To produce an unbiased assessment of the numbers and length frequencies of fishes, electrofishing was carried out within a 400 m net enclosure carefully laid out from a boat. The enclosure was fished thoroughly three times with a period of at least 30 minutes between each session. The fish were weighed and measured before being returned alive to the water.

Osprey diet was assessed from prey remains collected below feeding perches (trees, telegraph poles, etc) throughout the Reserve. The majority of remains were fish heads, although some tails and intact carcasses were also found. Remains could easily be identified to species by keybones (Plate 37), and the number of heads was taken as the minimal number of each species. The original size of the fishes was estimated from certain keybones for which bone length/fish length regression equations were calculated. Fish age was determined from growth marks on scales and opercular bones.

In 1990 and 1992, a total of 258 perch and pike were caught by electrofishing (Figure 55). The length frequencies of pike were almost identical in the two years, whilst fewer large (>25 cm) perch were caught in 1992.

Between 1990 and 1992, the remains of 239 pike and 173 perch were collected and, judging from their age, most were

probably sexually mature (pike 3–4 years; perch 3–12 years). The pike and perch taken by ospreys were of similar lengths, over a relatively narrow size range. Pike had a median length of 30 cm (range 18–48 cm) and perch 27 cm (13–42 cm). The length frequencies of pike taken in the three years were similar, whilst significantly more larger perch were caught in 1990 than in 1992. It is clear that ospreys select a particular size range of prey and do not take fish in proportion to their length frequencies, as determined by electrofishing (Figure 56).

Though of similar length, perch were on average about 1.5 times heavier than pike. However, ospreys appeared to eat more of the pike than the perch, as pike remains were primarily lower jaws and opercular bones whilst perch remains often consisted of whole heads attached to complete skins.

In 1991 and 1992 (when sufficient data were available), the proportions of perch remains decreased throughout the season (Figure 57), presumably in relation to their presence near the water surface. It may be that perch are more vulnerable early in the season as they bask near the surface.

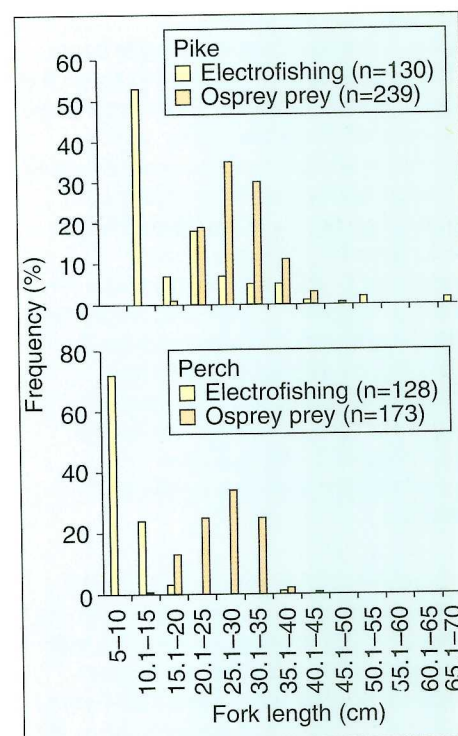


Figure 56. Comparisons of the length frequencies of fish caught by ospreys and by electrofishing. Ospreys took fish over a relatively narrow size range

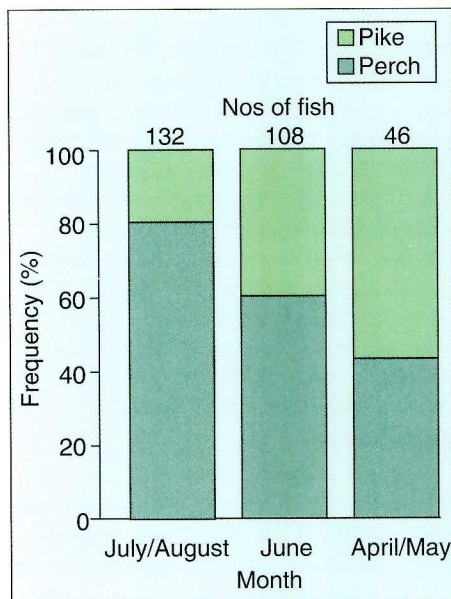


Figure 57. Seasonal changes in the proportions of pike and perch caught by ospreys. In both 1991 and 1992, the proportions of perch declined during the summer

There has been a significant change in the diet of ospreys since their recolonisation, with a reversal in the overall proportions of pike and perch. In the 1980s 79% of the prey items collected were perch, compared to 42% in the present study.

Results from this study suggest complex relationships between ospreys and their prey, even in a relatively simple system. The proportions of the two fish species in the diet have changed significantly in the decade since recolonisation, and in recent years diet has also been shown to change seasonally. Presumably both these long-term and seasonal changes are caused by changes in prey availability. Although ospreys take fish from a relatively narrow size range, the deep body shape of perch means that they are on average considerably heavier than the pike. The energetic values of such prey items are further complicated by the apparent unpalatability of certain portions of perch.

Osprey predation removes breeding pike and perch, but the subsequent effects on the population dynamics may be very different for the two species. Most of the pike taken were 3 or 4 years old, the youngest and smallest fish in the breeding population, whilst many of the perch were 5–12 years old, the oldest and largest breeders. The fecundity of both pike and perch is related to body

length, which is in turn related to fish age. Thus, in terms of the breeding population, the removal of many young pike may be less important than the removal of smaller numbers of considerably older perch. Ospreys may have altered the age composition of the perch population by removing the largest fish, which could explain the apparent reduction in the numbers of large perch in their diet. An alternative explanation could be that changes are not a result of predation but of the naturally cyclic nature of perch populations, an aspect requiring further study. However, previous ideas on fish population regulation in the Dinnet system need to be revised in the light of increasing osprey predation. Perch was formerly perceived to be relatively immune from predation (almost exclusively by other fish) after about three years.

D N Carss

Secondary plant compounds and herbivores

(This work was funded under the Joint Agriculture and Environment Programme)

Plant defences against herbivores – theoretical considerations

It is well known that herbivores select certain plant species in preference to others, but, even within species, some individuals are heavily browsed whilst others remain undamaged. These feeding preferences may reflect plant chemical composition, with the preferred plant species or individuals having the highest concentrations of nutrients and those rejected the highest levels of defensive secondary compounds. Thus, an important part of establishing the role of plant chemistry in herbivore preferences is understanding why plants differ in their allocation of available resources to these defence compounds. Early theories to account for such differences concentrated on the probability of a plant species being discovered by herbivores – their ‘apparency’ (Feeny 1976), but ignored several important constraints on plants, notably environmental resources.

The role of resources in plant allocation to defences was investigated by Coley,

Bryant and Chapin (1985), and resources have been specifically related to plant defences within a framework known as the ‘carbon/nutrient balance hypothesis’ (Bryant, Chapin & Klein 1983).

According to this theory, when nutrient levels are low, plants grow more slowly and the products of carbon fixation accumulate and are diverted to carbon-based defences, which therefore increase. This inverse relationship between secondary compounds and soil nutrients may be a result of low nutrient supply reducing protein synthesis which leads to an accumulation of phenylalanine, the precursor of phenolic biosynthesis. The theory also predicts that plants growing in low light conditions have low levels of photosynthate relative to tissue nutrients, and thus low levels of carbon-based defences.

There have been many studies of the link between resource availability and the concentrations of carbon-based defence compounds. However, many of them have focused on between- rather than within-species variation, and, when individual plant chemical composition was measured, the consequences for susceptibility to browsing were seldom examined. The lack of manipulative studies means our understanding of the chemical mediation of plant/mammal interactions lags far behind that of plant/insect interactions.

Against this background, ITE began a series of experiments to examine the links between environmental resources, variation in chemical constituents in individuals within a single plant species, and herbivore selection of these individual plants. One model system was Sitka spruce (*Picea sitchensis*) and red deer (*Cervus elaphus*) – a commercially important plant/herbivore interaction.

Four main questions are being addressed.

- What effect do environmental factors (ie soil nutrient levels and light availability) have on the chemical composition and morphology of Sitka spruce?
- How well do the responses of the trees to these two factors match the predictions of the carbon/nutrient balance hypothesis?
- What are the consequences of these environmental manipulations for the selection of individual trees by red deer?

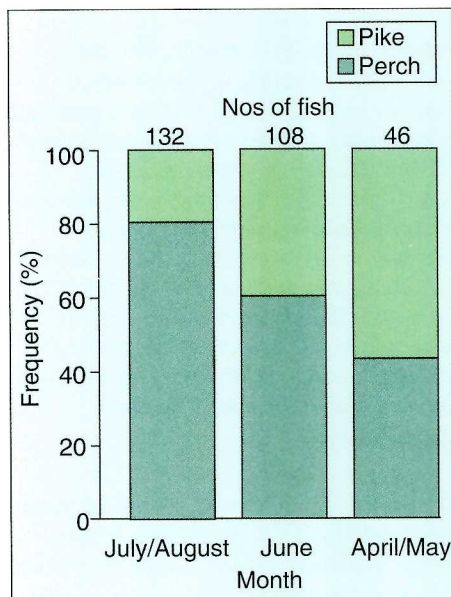


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Table 11 Experimental treatments applied to Sitka spruce seedlings

Treatment	Fertilizer level	Shade level
Control	1.1 kg m ⁻³ NPK ¹	No shading ²
Fertilizer	6.6 kg m ⁻³ NPK	No shading
Shaded	1.1 kg m ⁻³ NPK	30% incident light excluded
Shaded and fertilized	6.6 kg m ⁻³ NPK	0% incident light excludes

¹Fertilizer was slow-release nitrogen, phosphorus and potassium

²Light was excluded using green netting

- iv What effect do environmental factors have on the ability of the trees to recover after browsing, and for the allocation of defences to the regrowth foliage?

The response of Sitka spruce to environmental manipulation

In April 1990, 2000 15–30 cm Sitka spruce seedlings were planted in 9" pots, 500 were allocated to each of four treatments (Table 11). In March 1991, the effect of these treatments on tree chemical composition (Table 12) and tree morphology (Table 13) was measured. Where there was sufficient material, chemical measurements were carried out on the leaders and lateral shoots.

Both shade and fertilizer, particularly the latter, had large effects on both the morphology and the chemical composition of Sitka spruce seedlings. The two treatments usually interacted in their effects. Leading shoots tended to have lower concentrations of secondary compounds than lateral shoots.

The results largely support the predictions of the carbon/nutrient balance theory. Trees grown under low nutrient conditions had higher concentrations of total phenolics, condensed tannins, fibre and lignin, levels of tannins and phenolics decreased in the shaded trees. However, one group of carbon-based secondary compounds – monoterpenes – were not influenced by either nutrient levels or by shade.

The effect of tree chemical composition and tree morphology on deer feeding behaviour

To examine the response of deer to these environmentally induced changes in tree composition and morphology, we conducted a series of choice trials in which individual red deer hinds were offered an array of trees with each pair of treatment combinations (eg control vs

fertilized or shaded vs fertilized (Plate 38)).

There were 36 trials in all, six with each of six deer. During each trial, the time spent at each tree was recorded, together with the number of bites taken. After each trial, the weight of tree removed (corrected for water loss), the number of lateral shoots browsed, and the length of leader removed were measured.

Binomial regression was used to analyse the choice of trees visited by the individual deer. (The model assumed each tree has a particular probability of being visited depending on several factors, eg identity of the deer.) The probability of a tree being visited was strongly influenced by both the deer being tested and the position of trees in the experimental enclosure. Blocking factors were used in the model to remove these effects and to assess the role of the treatments in the probability of trees being visited. Only one variable tested – the number of lateral branches – significantly increased the probability of trees being visited. Treatment *per se* had no effect, ie there was no evidence that either fertilizing or shading trees significantly altered the probability of their being visited by deer.

Forward stepwise linear regression was used to assess the importance of

different factors in determining the weight of tree eaten, once it had been selected by the deer. Again, the deer being tested explained the amount eaten better than any other variable. The morphological variables – maximum span, tree height and leader twig width – significantly improved the fit of the model, but again fertilizer and shade had no influence on the amount eaten from individual trees.

These results show that deer decide both which tree to eat and how much to eat on the basis of morphological variables, and the treatments of shade and fertilizer have no effect other than via their effects on tree morphology. The evidence suggests that tree chemistry has little effect on deer feeding behaviour.

Effect of previous damage on susceptibility to further browsing – the role of secondary compounds

Despite the lack of response of the deer to tree chemical composition in our first experiment, the browsing of the trees may produce changes in the levels of secondary compounds, which may alter tree susceptibility to subsequent browsing. For example, in some plants, regrowth foliage is higher in secondary compounds because younger foliage is better defended. Also, the foliage produced after damage may have induced 'defences' and so be higher in secondary compounds. Again, these effects may be influenced by the soil nutrients available to the tree.

To test these ideas, we conducted a series of feeding trials with female red deer (hinds). The hinds were offered a choice between trees which had been damaged the previous year in experiment 1, and trees which had not

Table 12 Effects of treatments on tree chemical composition

Measurement	Effect of fertilizer	Effect of shade	Interaction between fertilizer and shade	Effect of branch (leading vs lateral shoots)
Nitrogen	▲	None	No	None
Water-soluble carbohydrates	None	▼	Yes	Leader ▼
Monoterpenes	None	None	No	(Not tested)
Total phenolics	▼	▼	No	Leader ▼
Condensed tannins	▼	▼	Yes	Leader ▼
Fibre	▼	None	Yes	(Not tested)
Lignin	▼	None	No	(Not tested)

▲ Significant increase in this measurement occurred

▼ A significant decrease occurred

Table 13. Effects of treatments on tree morphology

Measurement	Effect of fertilizer	Effect of shade	Interaction between fertilizer and shade
Tree height	▲	▲	Yes
Length of leading shoot	▲	None	Yes
Number of lateral branches	None	▲	No
Maximum span	▲	None	Yes
Width of needles on leading shoot	▲	▲	Yes
Twig with leading shoot	▲	▼	Yes

been browsed. In half the trials both damaged and undamaged trees had been previously fertilized, and in the other half they were unfertilized trees. Again, we measured biomass removed

from each tree and, because of the importance of tree size in preference (experiment 1), we expressed the amount eaten as a proportion of the tree biomass available. We also measured

the total phenolic levels in the leading shoots – in the case of the previously damaged trees, this foliage had regrown since previous browsing.

When trees had been fertilized, deer made no distinction between damaged and undamaged trees, eating the same proportion from each. However, in the case of unfertilized trees, the damaged trees were avoided, and almost twice as much was eaten on previously undamaged trees. Interestingly, the new shoots produced by the damaged control trees had a higher phenolic content than the equivalent shoots on undamaged trees; this increase in phenolic levels in regrowth foliage did not occur in fertilized trees. It is possible that this is one of the factors which influenced deer to avoid previously browsed trees – unless they had been fertilized. This pattern of phenolics in regrowth foliage also follows the predictions of the carbon/nutrient balance hypothesis: the most nutrient-stressed plants have the highest levels of carbon-based secondary compounds in their regrowth foliage.

Generally, it seems that the feeding preferences of red deer are governed by tree size and shape rather than by tree chemistry. However, under some circumstances, such as when trees have been grown in low nutrients and have also been previously browsed, secondary compounds may play an important role in deer feeding choices.

Our future work in this area includes an experiment using cloned Sitka seedlings of known browsing susceptibility to investigate the relative contributions of genetic and environmental constraints on the allocation of resources to secondary plant compounds.

S Hartley and B W Staines

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Plate 38. Red deer browsing on Sitka spruce tree

Experimental comparisons of the grazing behaviour of red deer and sheep

(This work was funded under the Joint Agriculture and Environment Programme, in collaboration with the Macaulay Land Use Research Institute)

In upland Britain, heather (*Calluna vulgaris*) moorland is increasingly being changed to grassland because of heavy grazing by large herbivores. It is well known that deer and sheep are selective both in where they choose to graze and in what they choose to eat, but observations in areas where the species graze alone suggest that the zonal pattern of their impact differs. This result would be expected from the differences between the species in body weight, overall size, mobility and resistance to windchill (hair vs wool coat). Differential impact has implications for management as, for a given area of moorland, the prescription for maintaining heather or spreading grassland, which can be achieved by controlling stocking rate or changing the distribution of preferred vegetation, will depend on which species is grazing.

To quantify the differences between red deer (*Cervus elaphus*) and sheep, and also the extent to which the distribution of grass patches modifies grazing behaviour, a major field experiment was designed. Red deer and sheep were grazed singly in 2.5 ha plots of three types; each type was replicated once and had the same total area of sown grass, but the grass was distributed in one large patch (76 m x 76 m), in four medium patches (38 m x 38 m), or in 12 small patches (22 m x 22 m) within a uniform heather sward. The experimental site was created in 1990–91 at Glensaugh, Kincardineshire, a hill farm run by the Macaulay Land Use Research Institute. The plots lay at 300 m, and the grazing behaviour was observed from the opposite hillside.

Several experiments were conducted in 1991–93; the experiment reported took place in May–July 1992, with three periods of grazing on a 14-day cycle. All plots received equivalent stocking on a body weight basis (7 deer and 11 sheep), and the three groups of deer and three groups of sheep each experienced all three patch treatments during the six weeks.

Both deer and sheep alternated between grazing and resting in several bouts each

Table 14. Contrasting effects of grass patch distribution on sheep and deer grazing

Plot type	1 patch		4 patches		12 patches	
	Sheep	Deer	Sheep	Deer	Sheep	Deer
% total time on heather	19	58	35	58	52	67
% grazing time on heather	9	40	26	36	43	48
Typical group size (nos of animals)	7.0	3.4	5.3	3.5	4.6	3.0

day, but the proportion of time spent grazing was greater in the late afternoon and evening than earlier in the day. Overall, sheep grazed for longer periods than deer, averaging 53% of daylight hours compared to 37% for deer. When grazing, sheep used the sown grassland more than deer (70% cf 57% of grazing observations), the difference being

most marked in the middle of the day; for both species, this usage was greater than expected from the extent of the grass patches. For resting, sheep also preferred sown grassland, but deer selected slightly for heather (53% and 84% of resting observations for sheep and deer respectively were on heather).

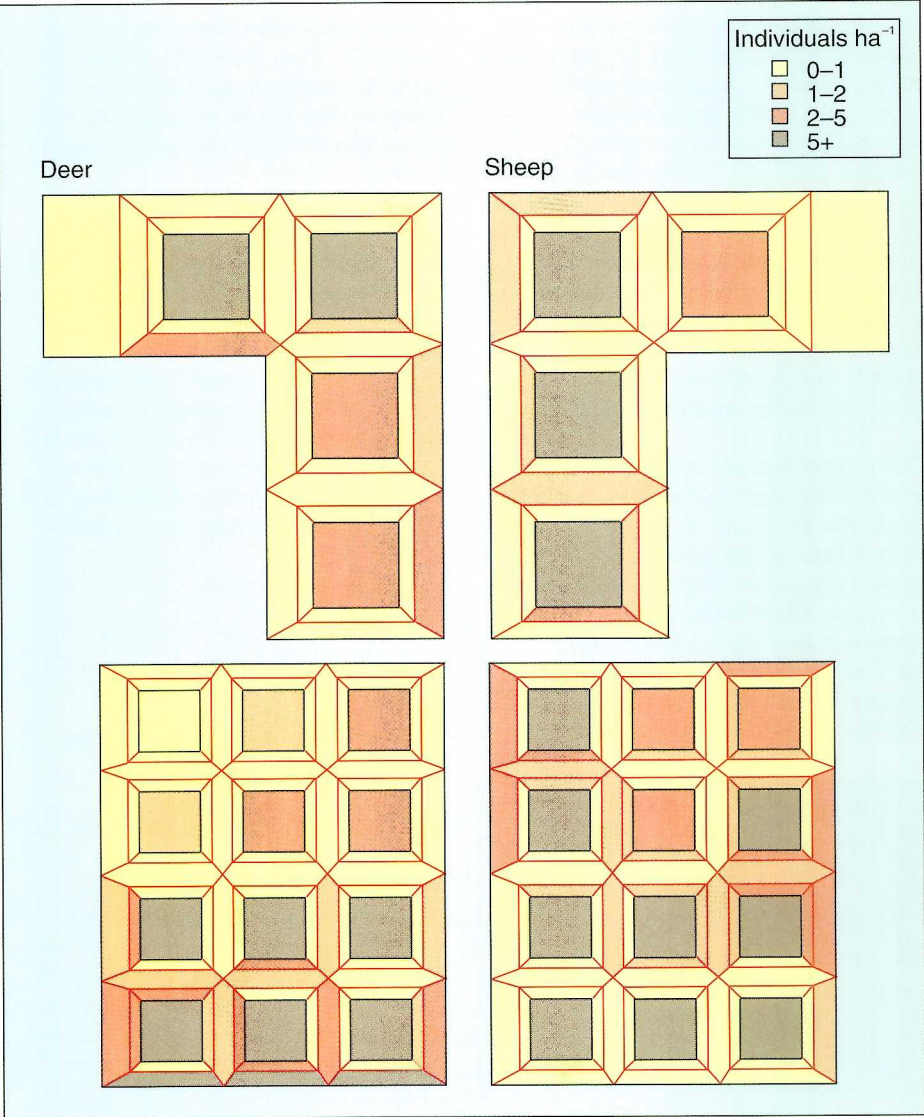


Figure 58. Average densities of grazing animals observed in a ten-day June period in grass patches and surrounding heather. The heather is divided into zone segments by dotted lines

The distribution of grass patches had a significant effect on the usage of heather by sheep (Table 14), but deer usage was little affected. Sheep spent more time on heather, and much more time grazing on heather, when the grass was in small patches spread over most of the plot. Grouping in the experimental herds was also affected by grass patch distribution, and significantly so for sheep (Table 14). All the sheep often grazed together on the one-patch treatment, but on the 12-patch treatment there were usually at least two groups.

The zonation of heather use was examined to find out where impact would be concentrated. Zones were defined by distance from the edge of the grass patch, viz 0–5 m, 5–30 m and 30+ m; this last zone was absent in the 12-patch treatment. As an example of the contrasting accumulated distributions observed, Figure 58 shows densities in the second grazing period for the replicated four-patch and 12-patch plots. Sheep showed a more consistent preference for the grass patches, whereas with deer three of the 12 patches were only lightly used in this period. Both species tended to have greater densities on the 0–5 m zone next to the grass, than on the 5–30 m and 30+ m zones. The 5–30 m distant heather was grazed most between the heavier-used grass patches; there was also greater usage between these and the perimeter fence, especially by deer.

The percentage of heather shoots grazed was estimated at the start and finish of each grazing period to assess impact. About twice as much heather was grazed next to the grass (the 0–5 m zone) than in the more distant zones (Figure 59) by both deer and sheep. Differences between the patch distribution types were significant only for the 0–5 m zone, heather utilisation being greatest in the

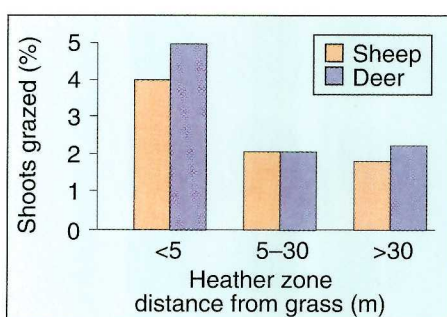


Figure 59. Percentage of heather shoots grazed in a ten-day period in zones defined by their distance from grass

plots with one large grass patch; heavier use was expected here because there was much less heather lying within 5 m of grass in this plot type. Although the zonal pattern in heather use did not differ between the herbivores, the overall utilisation of heather shoots was significantly greater for deer than sheep (means 2.9% and 1.9% respectively in a grazing period).

We conclude that the impact of sheep can be manipulated more readily than the impact of deer, by modifying the distribution of preferred vegetation. Heather next to grass receives the greatest utilisation and, where the preferred grass is concentrated into just one or a few patches, there will be greater pressure on the peripheral heather than on moorland with fragmented grassland. It is also evident that, at equivalent stocking rates on a body weight basis, deer will have a greater impact than sheep on heather moorland. Deer, however, generally occur in the British uplands at lower densities than sheep, so presently it is sheep that are most damaging upland heather.

Other experiments at this site have examined how deer and sheep behaviour and impact are affected by season, by stocking density, and by competition; the two species grazing together were compared with single-species grazing. As a step towards making management recommendations, further experiments have compared deer and sheep grazing heather swards which contained natural grass patches.

J L Clarke and D Welch

Tawny owl adaptation to habitat fragmentation

Most of Britain's natural habitats are now greatly modified and fragmented, which presents a problem to individuals dependent on the remaining habitat. What does an individual animal do when the patch sizes become smaller than its home range requirements? Consider the case of the tawny owl (*Strix aluco*) in the fenland of East Anglia. This is an agricultural landscape with trees occurring only in very small, isolated patches. Tawny owls are essentially woodland birds, which require trees not

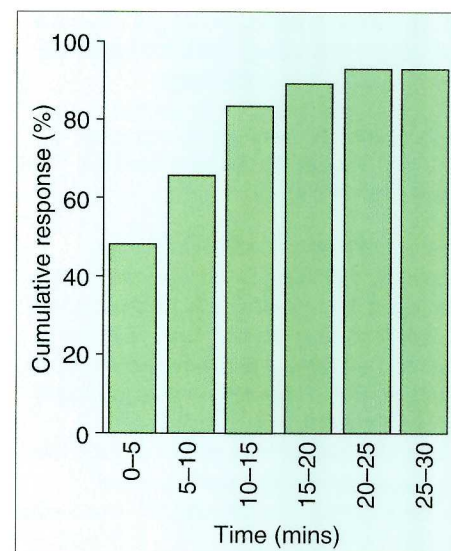


Figure 60. Cumulative percentage of known owls responding to imitation calls, based on 33 territories

only for nesting and roosting but also for hunting. They are 'sit-and-wait' predators, in that they sit on a perch and wait for prey (usually a small mammal) to appear. If, after a certain period, no prey has emerged, the owl flies off to the next perch and repeats the process until it makes a successful capture. The short, rounded wings of tawny owls also adapt them to woodland life, enabling them to fly among dense cover. Other species of owls which occur in more open habitats, such as the long-eared owl (*Asio otus*) and short-eared owl (*A. flammeus*), have longer, narrower wings.

Tawny owls respond well to imitations of their calls. In the autumn of 1990, 33 territories were located by listening for calling owls. The exact localities where owls had been heard were then revisited and the owl calls imitated for one minute in every five, for up to 30 minutes. Within this period, 94% of the owls had responded (Figure 60). From 1990 to 1992 tawny owls were censused by this method in woods ranging in size from 0.1 ha to 196 ha. Larger woods contained a number of different territorial pairs, whose areas could be mapped by hearing neighbours call simultaneously and by initiating territorial disputes (Southern 1971). This census revealed the distribution of occupied territories in the larger woods and throughout the fenland study area (Figure 61). Previous studies (eg Sharrock 1976) had indicated that tawny owls were absent from highly agricultural areas of the fenlands. However, the census showed that, within that area, owls were present in all woods

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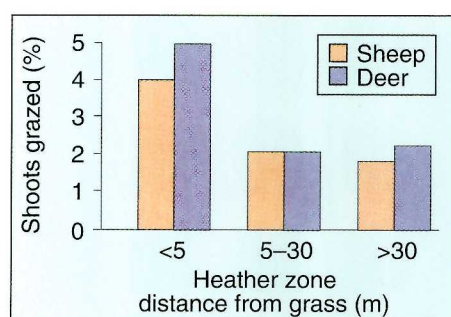


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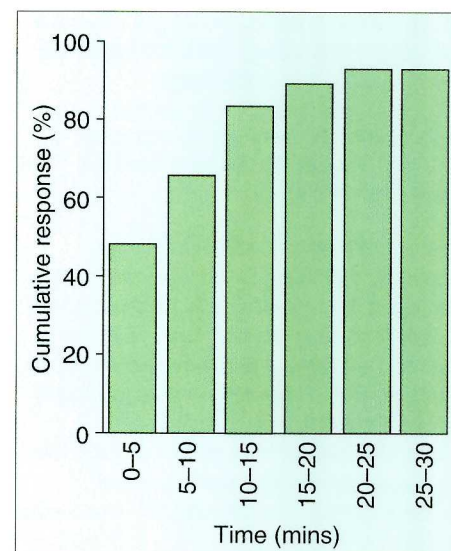


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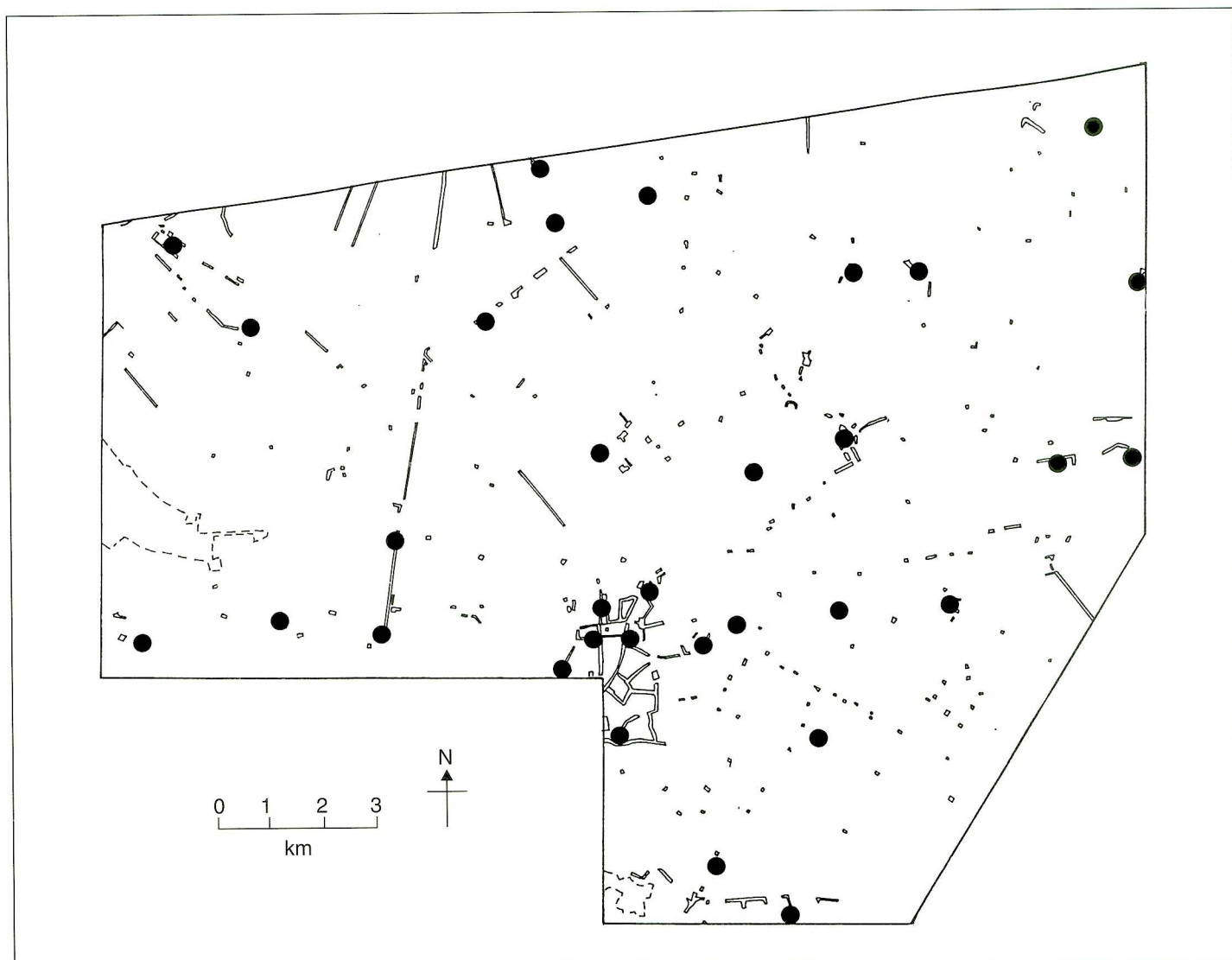


Figure 61. Distribution of territorial owls within the study area in 1992. All areas of woodland are shown and dots mark the centres of calling activity

over 4 ha and in some woods as small as 0.3 ha (Plate 39).

Once it was clear that tawny owls could persist in very small, isolated fragments of woodland, the next step was to see how they were able to survive in such a landscape. Over two years, 26 individuals were caught and fitted with radio-transmitters. Some of these were



Plate 39. A typical site containing tawny owls in the fenland area

in the 148 ha Monks Wood and the rest in the agricultural fenland. Radio-tracking gave information on the home range size, habitat selection, and activity patterns of individuals in both landscape types.

It soon became apparent that owls in open landscapes had much larger home ranges than those in Monks Wood (Figure 62). In both areas, male owls covered a wider area than females. Within their ranges, the fenland landscape was divided into four main habitat types: trees, farm buildings, arable land, and rough grassland (strips of grass without perches, by roads and ditches). When usage of these habitats by owls was compared to availability, individuals were shown to select the patches of trees and to avoid the arable land. Many individuals also selectively utilised the farm buildings, but more surprisingly many owls also hunted selectively the areas of rough grassland.

These areas had no perches and birds were apparently hunting from the ground. Unlike other owls which utilised these grassland patches (long-eared and

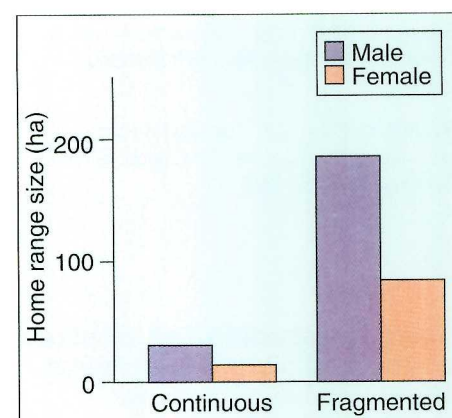


Figure 62. The winter (October–March) home range sizes of radio-tagged tawny owls in Monks Wood and fenland sites. Home range size was measured using the minimum convex polygon technique

barn owls), tawny owls only rarely hunted on the wing. The owls used these open perchless areas much more in the autumn, during and just after harvest, when small mammal densities were higher.

Continuous monitoring of individuals in both landscapes showed that owls in the fens were less active than owls in Monks Wood, as they spent longer sitting at each perch. The average time that individuals spent on each perch was not related to food supply, but was related to distance travelled between perches. Where perches were scarce and isolated, the costs of travelling between them would be greater, forcing individuals to spend longer at each perch. Overall, however, birds in the fens travelled 33% further each night than birds in Monks Wood. Evidently, owls in the fens expended more energy in foraging and travelling around their territories, and we might therefore expect the energy costs of living in this environment to be greater.

Although tawny owls are able to live out in small, isolated patches of trees, it is now important to measure whether they breed and survive as well in this habitat as in continuous woodland. Future work will concentrate on measuring the costs of habitat fragmentation on individual performance. The main surprise to emerge from existing findings, however, is the ability of these woodland owls to persist at all in such an open landscape, containing only small isolated clumps of trees.

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Fungal colonisation of straw: a study of patch dynamics

(This work was funded under the Joint Agriculture and Environment Programme, and involved collaboration with the University of Lancaster)

The distribution of organic resources and decomposer organisms in soil is not

Table 15 Outcome of pairwise interactions of fungi on agar, sterile soil and straw. The response is the fate of the responder to the challenger.

Responder	Challenger			
	<i>Agrocybe</i>	<i>Sphaerobolus</i>	<i>Chaetomium</i>	<i>Mucor</i>
<i>Agrocybe</i>	–	Deadlock	Wins	Wins
<i>Sphaerobolus</i>	Deadlock	–	Wins	Wins
<i>Chaetomium</i>	Loses	Loses	–	Loses
<i>Mucor</i>	Loses	Loses	Wins	–

homogeneous. The addition of organic resources (leaf litter, etc) is both periodic in time and heterogeneous in space. Thus, 'islands' exist of differing size, resource quality, and distances apart. The study of the invasion of these islands by decomposer organisms and their interactions is important for maintaining the fertility of soil.

The concepts of island biogeography (*sensu* MacArthur & Wilson 1967) have been applied particularly to communities of plants and animals in relation to habitat 'islands' within a mainland. Changes within these habitat islands or 'patches' (White & Pickett 1985) are emphasised under the term 'patch dynamics'. ITE is currently studying the applicability of the concepts and models associated with spatial (patch) dynamics in relation to describing the colonisation of organic resources by saprotrophic fungi and, specifically, with reference to straw fragments incorporated into soil. Most models and concepts associated with patch dynamics have been constructed from data on determinant organisms (animals and non-vegetatively propagating plants) where populations are readily quantifiable. In contrast, the hyphae of fungal thalli can link similar or different islands, allowing the transfer of materials between them via the fungal bridge. In this study, we have aimed to find some of the main factors determining the colonisation of the straw 'island' or 'patch' by fungi with a view to modelling island colonisation by non-determinant organisms.

Colonisation of straw patches *in vitro* by interacting fungal species

A range of fungi were isolated from wheat straw and cultured in the laboratory. A number of them were selected with different enzymatic capabilities and with different rates of hyphal extension. Isolates of microfungi, such as *Trichoderma* sp. and *Mucor heimalis*, had rapid mycelial extension rates, but could only utilise soluble

carbohydrates from the straw. Others, such as *Chaetomium globosum*, grew more slowly but had the capacity to decompose cellulose. The basidiomycete fungi, *Agrocybe gibberosa* and *Sphaerobolus stellatus*, were able to utilise lignin as a resource, in addition to cellulose (Robinson, Dighton & Frankland 1993).

A simple model of arrival at a new resource being dependent on fungal growth rate would suggest that the microfungi would colonise the resource at the expense of the basidiomycetes. However, because of differences in decomposing abilities, there is the possibility of alternative outcomes of competition, based on the ability of the different fungi to utilise the varied resources in the straw (substrate utilisation). The competitive interactions were first explored in culture where pairs of fungi were plated together in the same petri dish of malt agar, then in sterile soil, and finally in sterile straw pieces on unsterile soil. The interactions are shown in Table 15 and in Plates 40 and 41. From these data, it is possible to rank the four fungi tested in combative order using the interaction outcomes (with replacement being the strongest, deadlock intermediate, and intermingling the weakest).

Agrocybe > *Sphaerobolus* >> *Mucor* > *Chaetomium*

A scenario for the effects of these interactions in terms of decomposition of straw by a mixture of the four fungi can be hypothesised. *Mucor* would capture a primary resource (ie it would rapidly colonise and utilise the soluble carbohydrates available in a resource). The growth of *Chaetomium* would be slower, and, slowed even more by the presence of *Mucor*, it would not be replaced. The two basidiomycetes could replace the two microfungi, but neither *Agrocybe* nor *Sphaerobolus* could replace each other. The success of the two basidiomycetes as colonisers would

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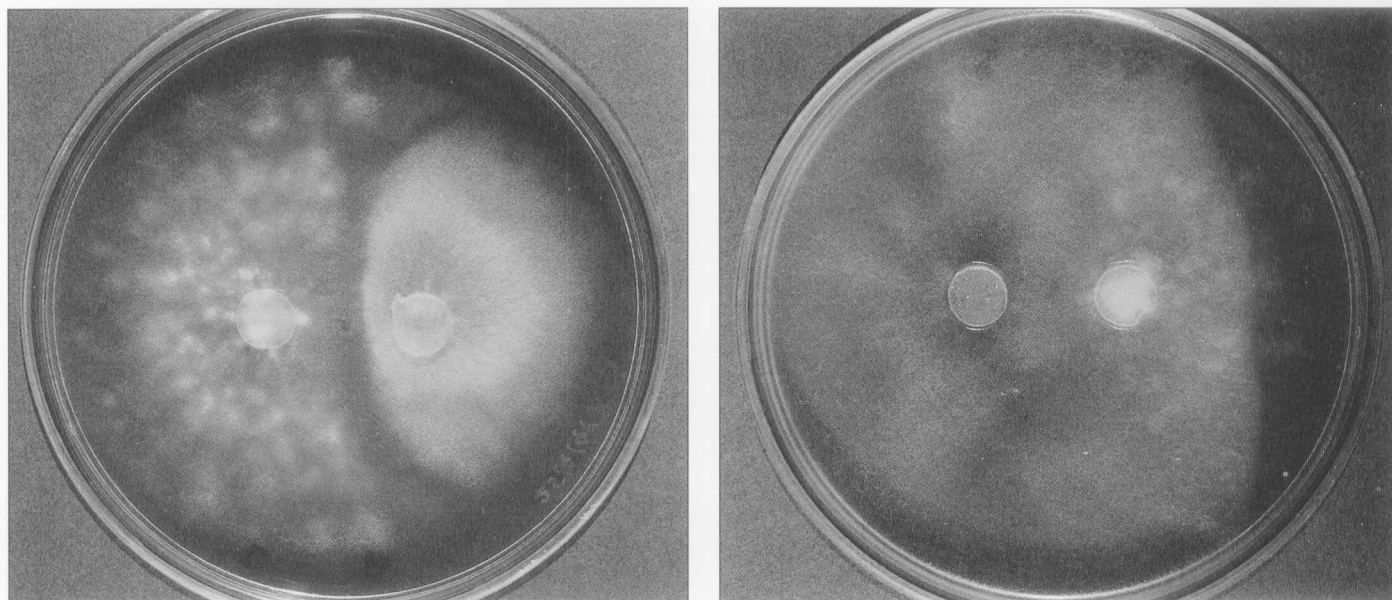


Plate 40. Interactions between fungi growing on agar: (i) deadlock interaction between *Chaetomium* (left) and *Agrocybe*, and (ii) replacement of *Chaetomium* (right) by *Sphaerobolus*

depend on the randomness of dispersal of their propagules in relation to available substrates.

Nutrient release from straw patches *in vitro* by interacting fungi

Outcomes of competition between the four fungi in terms of decomposition of straw as a resource were tested in laboratory conditions (Robinson *et al.* 1993). Pairs of fungi were inoculated on to sterile straw and incubated in microcosms. Fungal activity was assessed by measuring respiration and

decomposition, and the release (mineralisation) of inorganic nutrients was determined by measuring concentrations in leachate water. The values from fungal mixtures were compared with values of respiration expected from a 50:50 mixture of the two species. Observed respiration of mixtures of species were all significantly higher than that predicted, indicating that energy was being expended to maintain combative regimes; the increase was greatest in the *Agrocybe/Sphaerobolus* interaction where a deadlock interaction was being maintained (Figure 63). As

there were little differences in mineralisation rates from fungal mixtures compared with individual species, there was thought to be no synergism in the interactions.

Resource quality and fungal colonisation of straw patches

Different straw resources (leaves and internodes) were incubated in the field over the course of a year. Leaves have a lower lignin content than internodes and a lower C/N ratio. Thus, it is expected that this resource would decay more readily and support a different fungal

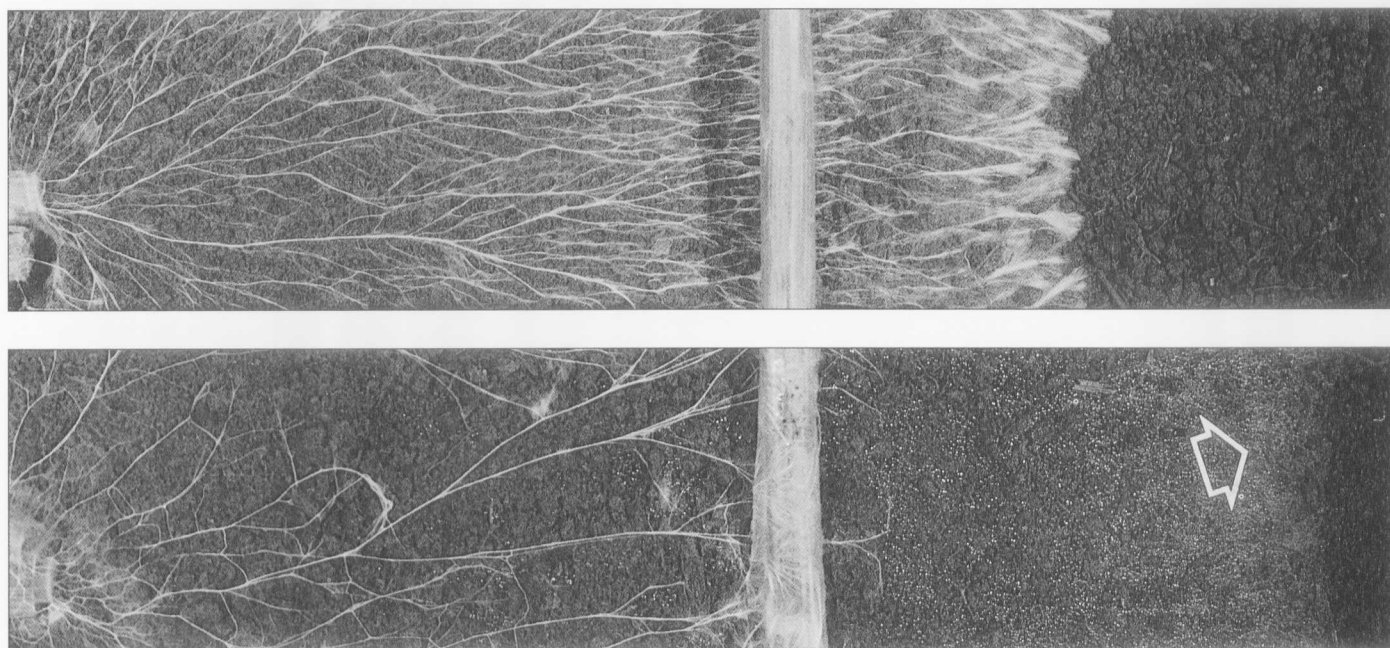


Plate 41. Interactions between fungi growing on sterile soil between straw baits: (i) deadlock between *Agrocybe* (above) and *Sphaerobolus* (below), and (ii) replacement of *Chaetomium* by 'non-diffuse' cords of *Agrocybe*, arrow indicates the mycelial front of *Chaetomium*

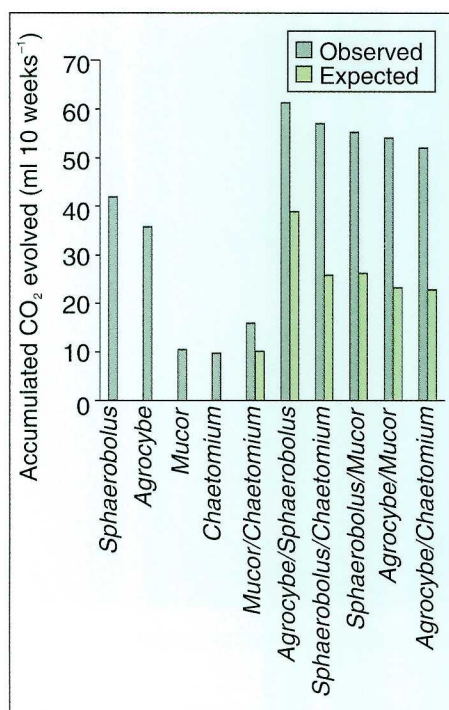


Figure 63. Accumulated respiration from single and mixed species of fungi decomposing straw. Red bars are the observed values; green bars are the expected values based on a 50:50 contribution to the total by each species of the interaction

community than internodes. Samples of litter were taken at different times of the year (Table 16), and it was shown that at the end of incubation (July) only 8% of the leaf litter remained, but 66% of the internode mass. Table 16 illustrates the different fungi isolated from litters at the three sampling times, showing distinct cohorts associated with each litter type and over time. These data demonstrate that the nature of the fungal community, allowed to develop naturally, can differ

Table 16. Most frequently isolated fungal taxa recorded from washed straw particles (% isolation frequency, n=120). Straw was incubated in the field and sampled at three times in the year. Taxa are tabulated according to association with each resource type and show differing cohorts with the progression of time

Species	Frequency of occurrence (%)		
	March	May	July
Most frequently on internodes			
<i>Cladorrhinum</i> sp.	27	0	0
<i>Fusarium culmorum</i>	12	0	0
<i>Fusarium</i> sp.	13	1	0
<i>Phoma</i> sp.	2	12	4
<i>Penicillium hordei</i>	0	11	2
Unidentified feathery	0	5	7
Most frequently on leaves			
<i>Cladosporium</i> sp.1	9	0	0
<i>Cladosporium</i> sp.2	15	1	1
<i>Epicoccum nigrum</i>	50	17	5
<i>Trichoderma</i> sp.	23	44	32

significantly on islands of differing resource quality and over time. The concept of resource preference is probably too simplistic, as it results from the outcome of competitive interactions determined by complex interactions of resource availability, enzymatic competence, rates of fungal growth, and mutual exclusion factors. From this study, we have identified that:

- mycelial extension rates of individual fungal species and species interactions affected patterns of colonisation of the straw 'patch' or 'island';
- the occurrence of the same fungal species was related to the different resource quality of the straw patch at each sampling time;
- particular assemblages of fungal colonisers differentially affected the release of plant nutrients and CO₂ release from the straw patch, an effect which also has implications for the extinction of species by decreasing island size (MacArthur & Wilson 1967).

These studies go some way towards addressing the problems of heterogeneity in soil by investigating the colonisation of resources by fungi. One of the main problems of studying fungi colonising organic substrates in soil is the inability to distinguish different fungal species. Although some are differentiated by morphological characteristics, there is a need for new methods for determining the presence and abundance of different types of fungi. To that end we are currently

investigating the use of DNA markers. In terms of modelling colonisation, we are collaborating with modellers at Imperial College, London, to parameterise a cellular automaton model for use in future studies of fungal colonisation of patchily distributed resources.

J Dighton, C H Robinson and J C Frankland

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- Transplanting species-rich grassland**
- Habitat restoration or reconstruction is generally concerned with producing interesting and attractive communities, thus differing from traditional land reclamation for agriculture, industry or housing. Because it involves the introduction of living material and not just physical shaping of a site, it may be described as community or ecosystem recreation. Four main strategies are used:
- habitat *creation* – usually starting with bare ground;
 - habitat *enhancement* – optimising the ecological potential of an impoverished site by suitable management or by introducing species;
 - habit *re-creation* or *reinstatement* – the restoration of a particular community after limited disturbance;

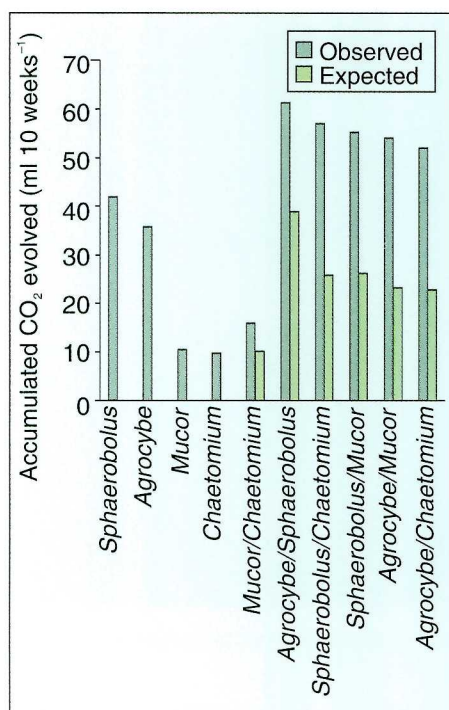


Figure 63. Accumulated respiration from single and mixed species of fungi decomposing straw. Red bars are the observed values; green bars are the expected values based on a 50:50 contribution to the total by each species of the interaction

community than internodes. Samples of litter were taken at different times of the year (Table 16), and it was shown that at the end of incubation (July) only 8% of the leaf litter remained, but 66% of the internode mass. Table 16 illustrates the different fungi isolated from litters at the three sampling times, showing distinct cohorts associated with each litter type and over time. These data demonstrate that the nature of the fungal community, allowed to develop naturally, can differ

Table 16. Most frequently isolated fungal taxa recorded from washed straw particles (% isolation frequency, n=120). Straw was incubated in the field and sampled at three times in the year. Taxa are tabulated according to association with each resource type and show differing cohorts with the progression of time

Species	Frequency of occurrence (%)		
	March	May	July
Most frequently on internodes			
<i>Cladorrhinum</i> sp.	27	0	0
<i>Fusarium culmorum</i>	12	0	0
<i>Fusarium</i> sp.	13	1	0
<i>Phoma</i> sp.	2	12	4
<i>Penicillium hordei</i>	0	11	2
Unidentified feathery	0	5	7
Most frequently on leaves			
<i>Cladosporium</i> sp.1	9	0	0
<i>Cladosporium</i> sp.2	15	1	1
<i>Epicoccum nigrum</i>	50	17	5
<i>Trichoderma</i> sp.	23	44	32

significantly on islands of differing resource quality and over time. The concept of resource preference is probably too simplistic, as it results from the outcome of competitive interactions determined by complex interactions of resource availability, enzymatic competence, rates of fungal growth, and mutual exclusion factors. From this study, we have identified that:

- mycelial extension rates of individual fungal species and species interactions affected patterns of colonisation of the straw 'patch' or 'island';
- the occurrence of the same fungal species was related to the different resource quality of the straw patch at each sampling time;
- particular assemblages of fungal colonisers differentially affected the release of plant nutrients and CO₂ release from the straw patch, an effect which also has implications for the extinction of species by decreasing island size (MacArthur & Wilson 1967).

These studies go some way towards addressing the problems of heterogeneity in soil by investigating the colonisation of resources by fungi. One of the main problems of studying fungi colonising organic substrates in soil is the inability to distinguish different fungal species. Although some are differentiated by morphological characteristics, there is a need for new methods for determining the presence and abundance of different types of fungi. To that end we are currently

investigating the use of DNA markers. In terms of modelling colonisation, we are collaborating with modellers at Imperial College, London, to parameterise a cellular automaton model for use in future studies of fungal colonisation of patchily distributed resources.

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- Transplanting species-rich grassland**
- Habitat restoration or reconstruction is generally concerned with producing interesting and attractive communities, thus differing from traditional land reclamation for agriculture, industry or housing. Because it involves the introduction of living material and not just physical shaping of a site, it may be described as community or ecosystem recreation. Four main strategies are used:
- habitat *creation* – usually starting with bare ground;
 - habitat *enhancement* – optimising the ecological potential of an impoverished site by suitable management or by introducing species;
 - habit *re-creation* or *reinstatement* – the restoration of a particular community after limited disturbance;



Plate 43. Turf being stripped from the donor site before being transported on pallets to the receiver site – October 1990

site a mixture of mat-grass (*Nardus*) grassland (U5d) and rush pasture similar to M25.

Turf translocation

Before turf translocation, the receiver sites were fenced to exclude rabbits, treated with total glyphosate herbicide ('Roundup'), and rotavated.

Two turf translocation procedures were used.

- i. (*Whole turf*) 100% translocation – whole turves, approximately 1 m wide x 2 m long and 8–10 cm thick, were stripped from the marked donor plots using a JCB and shallow backacter bucket (Plate 43), carefully placed on wooden pallets, then lifted on to a trailer using a tractor-mounted fork-lift. Following transport to the receiver site, the pallets were off-loaded and the turves laid over the same area of rotavated ground as that from which they had been taken.
- ii. (*Chopped turf*) 50% translocation – turf collected as above was spread out over twice the area of ground it had occupied at the donor site, and rotavated into the surface.

Turf from the donor plots was translocated to the 'dry' receiver plots using both the 'whole turf' and 'chopped turf' transfer methods in September 1990. It was not possible to use the 'chopped turf' method at the 'wet' receiver site at

this time as the ground was too wet and bumpy to allow rotavating in. The 'chopped turf' transfer of plot 3 was, therefore, delayed until September 1991.

Vegetation resurvey

Following initial survey of the donor and receiver plots, and nearby 'control' areas, prior to translocation, the vegetation was resurveyed in August 1991 and 1992.

Results

The NVC community type of the donor turves (MG5c) has been maintained on all the receiver plots over the two-year period since translocation (Table 17). There is little difference in 'goodness-of-fit' of the vegetation using the MATCH computer program (Malloch 1990) between 100% (whole turf) and 50% (chopped turf) transplants, and two years

after translocation they looked very similar (Plate 44). However, the retention of overall community structure hides a general decline in species richness between years one and two after transplanting (Table 18). In the first year, ephemeral species were able to invade patches of bare ground, especially in the plots where chopped turf had been spread over twice its area of ground. Subsequently, several key species have apparently disappeared, including petty whin and cross-leaved heath (*Erica tetralix*) from both the whole and chopped transplants of plots 1 and 2. Heather (*Calluna vulgaris*), cat's ear (*Hypochaeris radicata*) and heath grass have also been lost or have become severely reduced in cover. It is considered likely that the loss of some key species may be due to the absence of the planned cutting and removal of above-ground biomass from the trial plots in the early summer of 1992, which allowed the more vigorous species to dominate their less robust competitors. It is also possible, however, that the absence of the periodic flushing of the vegetation with base-rich water, which is believed to occur at Selar Farm, may have been a factor.

Conclusions

The turf transfers have been successful so far in retaining plant community composition. However, such is the rapid flux of species diversity and so tenuous is the hold of many of the surviving components of the donor vegetation that firm conclusions about the final success or otherwise of the turf transfer methods require a longer period of monitoring. The loss or reduction of key species, notably the genistas, highlights the difficulty in transplanting species with exacting ecological requirements.

Table 17. Relationship between NVC communities of whole and chopped turves translocated to the 'dry' and 'wet' receiver sites before their translocation in 1990, and 12 and 24 months later. Higher values indicate closer matches to named NVC community composition

			Year	
Plot		NVC community	1990	1992
'Dry' receiver site				
Plot 1	Whole turf	MG5C	50.5	60.6
Plot 1	Chopped turf	MG5c	50.5	56.9
Plot 2	Whole turf	MG5c	50.5	59.1
Plot 2	Chopped turf	MG5c	50.5	58.3
Control		U4b	54.4	54.7
'Wet' receiver site				
Plot 3	Whole turf	MG5C	51.8	53.1
Plot 3	Chopped turf	MG5c	51.7	46.8
Control		U5d	57.3	59.2

- iv. habitat *translocation* – the original community is moved wholesale from a donor to a receptor site.

Habitat translocation, the most ambitious and expensive option, has rarely been attempted and is only likely to be used when a site of high ecological value is threatened. It was used to relocate an area of grassland containing orchids at Stansted Airport (Anderson 1989) and for limestone grassland translocation in County Durham (Park 1989). In the present study, turf translocation has been used to test the feasibility of relocating vegetation of high conservation interest underlain by substantial coal reserves which could be extracted by opencast mining.

Selar Farm in West Glamorgan is a small, traditionally managed farm with unimproved mesotrophic grassland communities which are of sufficiently high conservation value to merit recognition and protection as a Site of Special Scientific Interest (SSSI). The farm consists of eight enclosures on boulder clay overlying Middle Coal Measures shales at an altitude of 200–300 m. The land slopes gently to the west and is drained by two streams. Soils of varying dampness support various grassland types, including mesotrophic, moor-grass (*Molinia*) and rush (*Juncus*) pasture. The commonest National Vegetation Classification (NVC) community is the mesotrophic heath grass (*Danthonia decumbens*) subcommunity of lesser knapweed/crested dog's-tail (*Centaurea nigra*/*Cynosurus cristatus*) grassland (MG5c), and it is the translocation of this community that is described here. Notable species recorded at Selar Farm include great burnet (*Sanguisorba officinalis*), petty whin (*Genista anglica*), dyer's greenweed (*Genista tinctoria*), and saw-wort (*Serratula tinctoria*).

The objective

The objective of the study was to determine the feasibility of translocating the vegetation from Selar Farm (the donor site) to a nearby receiver site.

Methods

Turf transplanting and seed collection and sowing were included in the trials, but this article refers only to the turf transplanting trial.

Donor site selection and survey

A range of vegetation types have been



Plate 42. The turf donor site at Selar Farm in July

transplanted, including the more widespread types and those of particular conservation interest. However, this article refers only to the latter.

Three 8 m x 2 m donor plots were selected for translocation from a field in which the 'special interest' lay in the unusual mixture of mildly calciphilous and calcifugous species, whose distribution seemed to be related to a small-scale shallow relief lying parallel with the slope and reminiscent of 'ridge-and-furrow' cultivation (Plate 42). Three mini-transects, each 3 m long, were set out at right angles to the 'ridge-and-furrow' for more detailed studies of soil/plant relationships. They were positioned with each end of a transect situated on a 'ridge' and the central portion crossing the 'furrow'.

Vegetation quadrats were recorded in the donor plots prior to transplanting, and along the mini-transects, and vegetation types ascribed to NVC communities. Preliminary investigations of the soil in the donor plots, involving auguring and pH analysis of the top 10 cm, indicated that soil type was a gleyed brown earth, pH 5.14–5.37. Surprisingly, bearing in mind the presence of calciphilous species, there was no evidence of base-rich areas in this field. However, the mean pH value of two water samples collected from the wet flush at the upper end of this field was 7.1. The base-rich water from this flush normally drains into the stream which runs along the northern edge of the field,

but a certain amount of lateral flow may occur, especially when the water table is high in winter, perhaps flooding the 'furrows' and thereby sustaining their relatively base-rich vegetation.

Receiver site selection and survey

Blaengwrach Farm is located approximately 1 km south-west of Selar Farm. It has also apparently been traditionally managed, although some of the pastures may have received inorganic fertilizers. The site has rather less conservation interest than Selar Farm. Blaengwrach Farm's advantages as the receiver site were:

- its proximity to the donor site;
- similar aspect and elevation;
- assumed similar low levels of soil nutrients;
- presence of a mire above the receiver site which might be used as a source of water for periodic flushing of plots to simulate the flushing which probably occurs on the SSSI at Selar Farm.

Two areas were used at Blaengwrach Farm: a 'dry' receiver site where the soil was an acid brown earth with pH 5.11, similar to that of the donor plots but more freely drained, and a 'wet' receiver site on a peaty gley soil, pH 4.02, which was a good deal wetter than the donor site.

Vegetation at the 'dry' receiver site was a species-poor calcifugous grassland (NVC type U4b) and at the 'wet' receiver



Plate 44. Chopped turf plot at the 'dry' receiver site two years after translocation

It seems at present that a higher proportion of species have been successfully transplanted to the 'wet' than the 'dry' receiver site. More effective cutting or grazing regimes might have prevented the loss of some species and the reduction in cover abundance of others, as might artificial flushing of the site with base-rich water. Further tests are planned to investigate these possibilities.

While there have been greater species losses from the chopped turf than the whole turf transplants in some cases, the differences have generally been small and there has been little variation where the rarer species are concerned. However, shrubby species have fared less well than grasses and herbs, perhaps because of their deep-rooting characteristics. The use of thicker turves

containing more root might have improved the successful translocation of these species. Because the chopped turf translocation technique is much easier and cheaper, involving movement of only half the amount of turf and not requiring it to be handled with the same care as when transplanting intact, it seems to be a very promising method for the translocation and re-establishment of grassland vegetation.

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Table 18. Summary of relative species richness of turves translocated to the 'dry' and 'wet' receiver sites before their translocation in 1990, and 12 and 24 months later

Plot		No. of species		
		1990	1991	1992
'Dry' receiver site				
Plot 1	Whole turf	40	34	31
Plot 1	Chopped turf	40	36	29
Plot 2	Whole turf	47	37	35
Plot 2	Chopped turf	47	49	40
'Wet' receiver site				
Plot 3	Whole turf	43	47	44
Plot 3	Chopped turf	43	–	52