Annual Report 1993–1994

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Natural Environment Research Council

Foreword

The past year has been one of considerable change in the Natural Environment Research Council, both in the focus of its science and in its structures. The catalyst for these changes was the publication of the White Paper *Realising our potential*⁻ a strategy for science, engineering and technology (Cm 2250). NERC was given a new mission for its science to embrace the concepts of meeting the needs of its user communities and contributing to wealth creation and the quality of life. We have, of course, always paid close attention to these objectives, but there is now a clear need for a sharper focus and better articulation of what we do in these areas. Basic science and long-term monitoring are also included in our mission, and due weight must be given to these when developing our science strategies.

The science directorates will cease to exist towards the end of 1994, and new structures will be put in place TFSD Institutes are being regrouped as the Centre for Ecology and Hydrology, with a unified ITE under a single Director However, the report of the Multi-Departmental Scrutiny of Public Sector Research Establishments is awaited, and decisions arising from this report may result in further organisational changes within NERC

An important activity during the year has been the preparation of a new science and technology strategy for the terrestrial and freshwater sciences. Publication is expected in July, and a number of research areas will be identified for priority support over the next five years.

This is my second and final foreword. During my relatively short time with NERC, I have come to appreciate and value the breadth and strength of our work in the terrestrial, freshwater and hydrological sciences Within ITE, for me, highlights of this year have been the report ansing from Countryside Survey 1990 and the launch of the Land Cover Map It is because of these, and very many other successes, that I am confident we can continue to produce high-quality and competitive science in the post-White Paper environment. Both ITE(North) and ITE(South) were visited by separate Science Management Audit Groups during the year. It is to the great credit of everyone involved in ITE that the reports of both groups recognised a continued advance in quality across the whole of the Institute over the five years since the previous visits

Finally, I should like to state how much I have appreciated the friendships that I have established with so many members of our community It is these that will be my most valued and lasting memories of NERC

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Director of Terrestnal and Freshwater Sciences Natural Environment Research Council

Report of the Institute of Terrestrial Ecology 1993-1994

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Natural Environment Research Council

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This Programme investigates the factors and processes that determine patterns of abundance through space and time in populations of single species and of communities of species. 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. In addition to the projects that are based at five ITE stations, the programme contains:

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

The Programme contains many projects having high scientific value as well as contributing directly to strategic research of both potential and immediate practical value, as the following five project reports illustrate. With the increasing exploitation of Scottish waters, both for fisheries and oil and gas production, the pressure on marine communities continues to increase, yet these communities are very difficult to study for logistic reasons. The first article summarises an attempt to come to grips with these difficulties by modelling the foraging activities of seabirds, one of the groups of top predators in the marine environment. As well as showing how realistic models used for predicting the effects of environmental change must be based on

a sound understanding of species biology, this article illustrates the increasing use made by ITE research teams of geographical information systems and of radio-transmitters that allow the activities of individual animals to be monitored over large areas. The second article illustrates how the study of basic ecological processes are vital if important environmental management issues are to be addressed realistically. Internationally, upland heathland is an increasingly fragmented and endangered habitat because of afforestation and overgrazing. In recent years, extensive areas of heathland have also been unexpectedly lost because of outbreaks of a moth whose larvae feed on heather (Calluna vulgaris) and other moorland plants, causing severe defoliation. Although the study points to the nutritional quality of the plant as an important factor affecting moth abundance, the increasing input of nitrogen, such as that arising from atmospheric pollution, and increasing ambient CO2, along with changing weather patterns, may combine to cause the moth to reach outbreak levels. The third article illustrates how long-term studies are required to disentangle the separate effects of environmental variables on organisms. The condition of toads (Bufo bufo) when they arrive at their breeding ponds in late winter has a critical effect on the number of young toads produced, and thus on overall numbers. Body condition, in turn, is determined by the joint action of the density of toads - which determines how strongly individuals compete for food, and of the environmental temperature which affects how much of their nutritional reserves the toads use before they arrive at the pond to spawn. Numerous factors have been invoked to explain changes in the numbers of amphibians, including habitat loss, exploitation, pollution and climate change. This is one of the few

studies to both monitor numbers and investigate the processes involved. The fourth article also illustrates the high scientific return that comes from welldesigned long-term programmes. The intriguing and intricate interactions between blue butterflies (*Maculinea* spp.) and red ants (Myrmica rubra) - in which, after feeding on a plant, the caterpillars of the butterfly then prey upon the larvae of the ant - have been modelled in a way that allows both spatial variations in the abundance of the foodplants and the incidence of unpredictable environmental influences to be taken into account. Not only will this model improve our understanding of complex systems of interacting species - in this case, plants, butterflies and ants – but it also allows us to predict the effects on the abundance of each species of habitat manipulation, such as changing the intensity of grazing or of adding or removing plants. The final article also considers the interactions between plants and animals. Long-term studies of scrub succession on a nature reserve showed that plots of land cleared of secondary woodland did not progress to scrub, as had been expected, the apparent reason being that fallow deer (Dama dama) browse the young woody plants. This hypothesis was confirmed by experiments in which deer were excluded from certain areas; compared with sites where browsing was allowed, the woody plants were very much taller in the protected enclosures, with some species of plants being more affected than others. Deer damage in nature reserves has been recorded before, but this is the first study to demonstrate that deer can have a marked effect on the vegetation in areas managed specifically for shrubland succession.

J D Goss-Custard

Plate 41. Black guillemot on the Island of Foula

Modelling environmental effects on seabird foraging energetics

(This work was funded partly by an award from the Leslie and Dorothy Blond Trust)

With the increasing exploitation of Scottish waters, both for fisheries and oil and gas production, comes increasing pressure on marine communities. Seabirds are easier to study than other top predators (seals, dolphins and whales), but even they are difficult and expensive to survey at sea. We are investigating whether we can identify their critical feeding habitats by calculating the times and energies they would need to use all along the Scottish coast, and by assuming they will concentrate in areas where their time costs are low and their net energy returns high.

Most marine birds are colonial breeders but, even within a species, the number of pairs breeding at a colony varies greatly. Several factors have been suggested as limiting population size: competition for local food supplies near breeding colonies, availability of nest sites, and density-dependent factors operating outside the breeding season. Ricklefs (1990) concluded that current hypotheses based on these factors are generally untestable with existing data, and stressed that more appropriate hypotheses and extended data sets are needed. Recent events, for instance the large-scale breeding failures of Shetland seabirds in the 1980s and the Braer disaster in 1993, have further highlighted our lack of knowledge of the requirements of seabirds. This poor understanding limits our ability to predict the consequences of changes, either long-term or catastrophic, in the marine ecosystem.

The complex spatial nature of seabird breeding and feeding distributions has been a major obstacle to developing suitable models, and only in the last few years have mathematical techniques, combined with the enormous power of modern computer work-stations, enabled progress to be made. In particular, the development of geographical information systems (GIS) now routinely permits tasks which would have been nearly impossible ten vears ago. We have extended our preliminary GIS models of the relationships between seabirds and the marine environment, using a training award from the Leslie and Dorothy Blond Trust.

Our study area covers the coast and inshore waters of east Scotland. It includes a wide range of coastal habitats that hold important concentrations of many species of seabird. It also has several areas where seabirds are potentially at risk: from oil tanker traffic in the Firth of Forth, from oil production industry in the Moray Firth and from the rapidly expanding industrial fishery for sandeels (*Ammodytes* spp.). Sandeels are a key prey item for many seabirds and other marine top predators.

Information on seabird breeding colonies (location, species and numbers), both on the coast and offshore islands, was obtained from the Colony Site Register of the Joint Nature

Conservation Committee, and bathymetry and seabed sediment data, for an area extending 50 km offshore, were taken from British Geological Survey maps. These data were digitised and stored in a GIS. The area was classified by both depth zones (0-10). 10-20, 20-30, 30...., 200 m) and sediment type. Sandeels are almost always found associated with sandy substrates. The area was, therefore, initially reclassified into just sandy and non-sandy areas. It was further subdivided by a grid of 1 km x 1 km cells to produce small polygons (<1 km²) of known depth, sediment type and location. Colony locations, sediment and bathymetry characteristics are illustrated in Figure 56.



Figure 56. The locations of shag colonies (red dots) and, within their 10 km feeding ranges (blue outlines), seabed sediments (yellow sand, preferred sandeel habitat) and 0–60 m depth bands (blue on yellow). The inserts show details for Moray Firth and Firth of Forth (Computer cartography at ITE Banchory by P J Bacon)



Plate 42. The shag is a member of the cormorant family which feeds mainly on sandeels caught near the seabed. The species is endemic to the North Atlantic and suffers heavily from food shortages and man-induced disasters (eg *Braer* oiling incident)

The shag (*Phalacrocorax aristotelis*) was selected as a test species (Plate 42). This seabird is particularly sensitive to changes in food availability and ITE's seabird studies at the Isle of May have collected much information on its foraging requirements and energetics (Wanless *et al.* 1993). Shags feed mainly on sandeels, which they catch on or near the seabed.

Small, powerful radio-transmitters allow us to track shags from their nests to their feeding grounds, and the loss of the radio signal when the birds dive lets us record remotely details of the feeding behaviour. The energy costs of foraging are principally those of flying to a site and the cost of diving to the seabed to forage, which depends on the water depth there. However, while flight costs increase linearly with distance, dive cycle time (dive time plus recovery time on the surface) increases rapidly and exponentially with water depth: consequently, dive cycles in deep water use disproportionately more energy than those in shallow water.

We used our empirical data to predict daily foraging time and energy for a range of realistic activity budgets. Figure 57 shows predicted daily foraging times for a range of foraging distances (1–20 km) and water depths (1–50 m) typically used by shags. Figure 57i represents a breeding season with 'good' feeding conditions (energy requirements met by making 45 dives per day during three foraging trips); Figure 57ii refers to 'poor' feeding conditions (150 dives per day, two foraging trips).

These time and energetic data were integrated with the spatial information to predict total daily time and energy costs associated with foraging at any location, given the water depth there and its distance from the nearest breeding colony. The results, expressed as time costs for good and poor conditions, are illustrated in Figure 58. As shags do not feed at night and one member of the pair is always present in the colony incubating or brooding the young, the maximum foraging time for an individual is normally less than seven hours. Thus, even in



Figure 57. Predicted daily foraging efforts of shags in relation to foraging range (km) and water depth (m). Flight speed taken as 13.2 m sec^{-1} and dive time plus recovery time on the surface given by: Dive_time (sec) = $e^{3.61 + 0.0405 + depth.(m)}$

Predictions for: (i & ii) daily feeding time (DFT), hours; (iii & iv) daily energy expenditure (DEE in multiples of standard basal metabolic rate). (i) & (iii) assume 'good' feeding conditions (=15 dives trip⁻¹ and 3 trips day⁻¹), while (ii) & (iv) assume 'poor' feeding conditions (=75 dives trip⁻¹ and 2 trips day⁻¹). Note the large effect of feeding conditions on necessary effort





(Computer cartography at ITE Banchory by C Needle & P J Bacon)

good feeding conditions, the model predicts that shags breeding at colonies in east Scotland are restricted to inshore waters, while under less favourable conditions the area contracts even further and is concentrated mainly in shallow water within 5 km of the coast.

In the results presented above, shag foraging energetics have been modelled such that variation in just two parameters (water depth and distance to the nearest breeding colony) are incorporated to estimate total daily foraging time or energy costs. A third parameter, seabed substrate type, can also be introduced, with suitable feeding area restricted to areas with sandy sediments, the assumption being that sandeel distribution will be closely associated with such areas.

As an initial test of the shag foraging model, we developed an earlier hypothesis of Cairns (1989). This assumes that birds from neighbouring colonies typically occupy nonoverlapping feeding zones (hinterlands) and predicts that the number of birds breeding in a colony is a function of the size of these hinterlands. Cairns demonstrated that the number of shags nesting in colonies in Orkney and Shetland were positively and significantly correlated with hinterland size. We repeated Cairns' analysis using the east coast of Scotland but extended the model to test for the effect of water depth and sand, first ignoring distance from the breeding colony and then incorporating travel costs using the energetics models. The length of coastline occupied by the colony was also included as an independent variable.

A routine analysis did indeed suggest that environmental and energetic variables had a significant effect on shag colony size, but closer inspection of the data revealed that the apparent significance was due principally to bias exerted by a single large colony on the Isle of May. Removal of this colony from the data set resulted in a marked reduction in the amount of variation explained, and most analyses of the other 80 colonies excluding the Isle of May were either not significant or only weakly significant.

Environmental variables, therefore, appear to be rather poor predictors of shag colony sizes in east Scotland. However, this may be because some colonies are safer nesting sites or have more dependable food in years of regional shortages. A more critical test of our energetics models will be to compare predicted feeding distributions with observed distributions of shags at sea. This test requires development of models to distribute the shag population over the potentially usable habitat in relation to energy costs, habitat suitability and feeding competition. These predicted distributions will be compared with observed distributions of shags at sea, through collaboration with other organisations.

It is clear that GIS is a powerful management tool. It directly allows the identification of key marine areas and can highlight those prone to environmental changes and damage (eg sediment deposition or removal by industry; oil installations; pollution; changes in fisheries practices). In combination with the spatial foraging models we are developing, GIS can be extended to assess the consequences of such impacts on the feeding areas and population sizes of seabirds.

P J Bacon, C Needle, M P Harris and S Wanless

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Winter moth outbreaks on Scottish heather moorlands – a new problem

(This work was funded by the Aberdeen Research Consortium, the Leverhulme Trust, the Scottish Landowners Federation, Scottish Natural Heritage and the Royal Society for the Protection of Birds)

Upland heathland represents an increasingly fragmented and endangered

habitat type, both within Scotland and internationally. Afforestation and overgrazing are major causes of the decline of heather (*Calluna vulgaris*) cover, but defoliation of heather by outbreak populations of phytophagous insects can accelerate this loss.

In recent years, extensive areas of heathland in NE Scotland have been lost due to outbreaks of the winter moth (Operophtera brumata) (Plate 43). Although the winter moth is well known as a pest of broadleaved trees, outbreaks on areas of open moorland represent a relatively new phenomenon, being first recorded in Orkney in 1980 (Picozzi 1981). Within moorland outbreak sites, high densities of winter moth larvae feed on heather (and other moorland plants such as blaeberry (Vaccinium myrtillus)) during May and June and cause severe defoliation. Defoliated stands of heather rapidly dehydrate and die, and may be replaced by invasive grass species. Regeneration of heather is typically poor on outbreak sites and the most severely affected areas, usually found at altitudes over 600 m. may extend over hundreds of acres.

Adult moths are active in November and December. The flightless females climb to the tops of moorland plants and mate before laying eggs in crevices on the plants or amongst ground litter. The larvae usually hatch in late April; newly hatched larvae disperse by spinning silk threads and drifting on the wind. They feed until late June, when they pupate in the soil until winter.

Objectives of current research

Winter moth outbreaks can cause serious and lasting damage to large areas of upland heathland, so it is clearly important to determine the reasons for the recent development of these outbreaks and whether they are likely to become more severe and widespread in future years. ITE has, therefore, initiated a research programme, in collaboration with the University of Aberdeen, to determine the factors which influence winter moth survival and development upon heather moors. The study has the following main objectives:

- to develop monitoring techniques to determine adult and larval winter moth population densities on outbreak sites;
- to define winter moth phenology, feeding behaviour and development on heather moorlands;



Plate 43. Male winter moth

- to assess the role of host plant chemistry in determining winter moth survival and development upon heather moorlands. Host plant nutritional quality is an important influence in insect performance and an improvement in plant quality may be a contributing factor to outbreak formation. Certainly the occurrence of winter moth outbreaks upon heather moorlands is surprising in this context, as heather is likely to be nutritionally inferior to many of the more usual broadleaved winter moth foodplants.
- to examine the potential effects of the environmental changes currently affecting the uplands upon winter moth survival and development. There are increasing nitrogen inputs in the uplands due to atmospheric deposition and rising carbon dioxide levels. These changes may affect the chemical composition of upland plants, and the performance of the insects which feed upon them. (For example, increases in carbon dioxide levels may lead to increased levels of carbon-based defensive compounds in plants, and hence to reduced food quality.) Shifts in insect distributions, population densities and host plant range may serve as early indicators for such environmental changes.

Population studies

The numbers of emerging adult moths in a badly affected moorland outbreak site in NE Scotland were measured in



Plate 44. Assembling sticky traps to monitor winter moth numbers at a moorland outbreak site in NE Scotland

November and December in 1992 and in 1993, using sticky traps (Plate 44). Larval densities were compared on two potential winter moth foodplants, heather and blaeberry, at the same site. The results (Figure 59) indicate that larval densities were generally higher in areas of mixed heather/blaeberry vegetation than in areas which were dominated by stands of pure heather or pure blaeberry. Both



Figure 59. The densities of winter moth larvae (caterpillars m⁻⁻) at an outbreak site in NE Scotland on 14 June 1993. Results are shown for stands of blaeberry and of heather growing alone (pure). and for predominantly blaeberry with some heather and predominantly heather with some blaeberry (mixed)

plant species were heavily defoliated at this site, and it is likely that they both play a role in winter moth outbreak formation. Most outbreak sites so far examined in NE Scotland have occurred upon mixed heather and blaeberry moorlands.

However, despite the extremely high densities of feeding larvae observed during June 1993, the numbers of adult female moths that subsequently emerged from their underground cocoons was lower in 1993 compared with in 1992 (Figure 60). The most likely explanation is that the earlier snow falls in 1993 disrupted the normal winter moth emergence and mating patterns. Figure 60 suggests that female emergence, which typically takes place several days later than male emergence, was particularly affected by this factor. The effect of this disruption upon the population densities of larvae in 1994 has still to be determined.

Larval performance upon alternative moorland host plants

Feeding trials were conducted in order to determine the effect of host plant selection on winter moth survival and development. Larval survival was considerably greater when they were reared on blaeberry alone than when they were reared on heather, and subsequent pupal weights were also about 10% higher upon blaeberry. In Lepidoptera, pupal weight is tightly correlated to adult size and fecundity: the wing spans of moths that were reared on heather as larvae are smaller than those of moths reared on blaeberry, Sitka spruce (*Picea sitchensis*) or oak (*Quercus*) (Figure 61).

Larvae fed on heather produced more frass per unit weight of food eaten than those fed on blaeberry, which indicates that heather was less digestible. The results of these rearing experiments confirm our hypothesis that heather represents a nutritionally suboptimal food plant for the winter moth. Previous work (Iason, Hartley & Duncan 1993) has shown that heather has a relatively low nitrogen content and high levels of defensive compounds such as phenolics



Figure 60. The cumulative numbers of male and female winter moths emerging in 1992 and in 1993, measured using sticky traps



Figure 61. Frequency distributions of male wing lengths of moths taken from different host plants, namely heather, blaeberry, Sitka spruce and oak (data for the moths from Sitka and oak provided by S Fraser, NERC Centre for Population Biology, Imperial College at Silwood Park)

and tannins. The presence of blaeberry in moorland areas is likely to enhance larval survival and development, and may thereby increase the probability of outbreak formation.

Conclusions and future research

The results so far are consistent with the view that the nutritional quality of the host plant is an important influence upon winter moth survival and development. The presence of blaeberry may be one factor which enables the winter moth to attain outbreak population levels in an apparently unfavourable habitat type.

However, this factor cannot provide a full explanation for the recent prevalence of these outbreaks. A more detailed study of host plant tissue chemistry and its effect on larval development is necessary. Future work will concentrate upon the effects of increasing nitrogen inputs (such as those from increasing atmospheric pollution) and increasing ambient CO₂ levels on host plant biochemistry and subsequent winter moth performance.

In fact, the results from our study of adult moth emergence (Figure 60) suggest that weather patterns (eg date of first frost/ snow fall, length of snow lie) may also be an important influence on the dynamics of winter moth outbreaks, but the data to demonstrate this conclusively will take many years to collect. Meanwhile, we will continue to use the study of basic ecological principles (the role of food quality and host/plant switching in population increases of pest species) to address important management, economic and conservation problems.

S E Hartley and J Kerslake

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The effects of environmental temperature and population density on common toad body condition

In northern latitudes some mammals and all reptiles and amphibians avoid the potentially lethal conditions of winter by hibernating. This physiological adaptation to prolonged periods of food shortage and severe environmental conditions is recognised as a time of particular stress and one from which many animals do not survive. Animals prepare for winter by accumulating energy reserves, stored as lipids, glucose and glycogen, which are then utilised during hibernation (Koskela & Pasanen 1975). Metabolism in poikilotherms, such as amphibians, is correlated with temperature (Ryser 1989), and therefore it is feasible that cold winters may be less stressful than relatively warm ones because the utilisation of energy reserves will be lower. A rise in metabolic rate during hibernation will result in a decline in body weight for a given length (condition), and ultimately in death. Clearly, the body weight of an animal entering hibernation will be one factor affecting its ability to survive. Changes in body weight are related to food intake and this may be density dependent (Denton & Beebee 1993).

Many aspects of the life cycle of the common toad (Bufo bufo) (Plate 45) make it a good animal for studying the possible effects that population density and environmental temperature may have on body condition and survival. Not least of these is the relative ease with which large numbers of adults can be captured every year at ponds where they congregate to breed immediately after emergence from hibernation in early spring. In addition, there is now considerable worldwide concern about the decline of some amphibian populations and its underlying causes, one of which may be climate change (eg 'global warming'). In order to study any effects that changes in climate or density may have on body condition and survival, long-term studies are required and these are, unfortunately, rare



Plate 45. Paired male and female common toads and a single 'satellite' male



Plate 46. Paired male and female common toads arriving at the breeding pond in early spring. Common toads exhibit sexual size dimorphism which can be clearly seen, with a relatively small male amplexed with a much larger female

However, one long-term study (1979present) of common toads breeding (Plate 46) at a pond in south Dorset measured routinely the body length (snout-vent) and body weight (1983present only) of all adults, and recorded numbers. As a result, it has been possible to investigate changes in body condition in relation to toad density and environmental temperatures, particularly those occurring during the winter. Four categories of adults were recognised depending on their sex and whether or not they were first-time breeders (0-yr) or animals that had bred previously (>0-yr). With the exception of Table 10, data relating mainly to males are presented here.

Body condition

Body condition is usually accepted as body weight standardised for body length, and here is defined as the ratio of observed weight to 'expected' (average) weight for a given length – so that average condition is represented by a ratio of one. The condition of toads from different years was compared after first deriving an overall relationship for 'expected' (average) weight, given length, for all years combined and also for each toad category.

When plotted (Figure 62), the data showed that there had been an overall decrease in condition since 1983. One-way analysis of variance for differences in average body condition between the 11 years of the study and both Spearman rank and ordinary correlations between average condition and year of study were all significant for each toad category (Table 10). With the exception of >0-yr females in 1987 and >0-yr males in 1990, toad condition was higher than average during the first five years of the study (1983-87) and lower than average during the latter six (1988–93). The pattern for females was similar to that shown by males.

Table 10. Significance (probability, P_a) of one-way ANOVA for differences in the average body condition of the four toad groups between years (n=11); Spearman rank (r_s) and ordinary correlations (r) between condition and year of study, together with their significance levels (p_s and p_i)

Toad group	Р	$\Gamma_{\rm s}$	(p ₃)	r	(p ₁)
0-yr male	<0.001	-0.87	< 0.001	-0.86	< 0.001
>0-yr male	< 0.001	-0.86	< 0.001	-0.87	< 0.001
0-yr female	< 0.001	-0.87	< 0.001	-0.89	< 0.001
>0-yr female	<0.001	-0.83	< 0.002	-0.73	<0.011

Of the two components of body condition, it is body weight rather than length that is capable of both increasing and decreasing in response to a stress resulting in changes in condition. The two most likely forms of stress that will affect toad body weight are food availability, which may depend on how many other toads are competing for the same resource, and environmental temperature, as this will affect metabolic rate and therefore the rate at which stored energy reserves are utilised.

Toad density

Only a fraction of the total number of toads present in the habitat breed each year and, therefore, if competition for a resource that affects body condition occurs, then the number of these nonbreeding animals must be estimated: 34% of males were estimated to breed first at the age of four years and 85% between the ages of three and five (Reading 1991). First-time breeding in females typically occurs one year later than in males, with an estimated 71% doing so at five years (range: 4–6 years).

After allowing for differences in the age of sexual maturity between males and females, and taking into account the known number of breeding adults each year, annual estimates for the total



Figure 62. Pattern of change in the body condition (\pm 95% CI) of 0-yr and >0-yr male common toads between 1983 and 1993. The value '0' represents the overall mean body condition of all male toads in each category for the period 1983–93

Correlation with year:

0-yr: r=-0.86; P<0.001; n=11 >0-yr: r=-0.87; P<0.001; n=11



Figure 63. The relationship between male body condition and toad density for 1983–89 0-yr males: r=-0.74; $r^2=55\%$; n=7; P=0.057>0-yr males: r=-0.83; $r^2=69\%$; n=7; P=0.021

number of toads present in the habitat were obtained. Regression analysis revealed that 55–69% of the variation in male body condition could be explained by toad density (Figure 63). Because of the greater minimum age at sexual maturity in females, it was only possible to estimate the total toad density for the seven years from 1983 to 1989. The pattern in females was similar, with toad density explaining 45–58% of the observed variation in body condition. It is



Figure 64. The relationship between male body condition on arriving at the breeding pond in spring and the mean temperature of the month preceding the start of spawning (mT.Sp-1) 0-yr males (excl.1991): r=-0.70; $r^2=49\%$;

n=10; P=0.024

>0-yr males (excl.1991): r=-0.61; r²=37%; n=10; P=0.061 notable that in all toad categories the three years resulting in the worst average body condition were the years with the three highest toad densities.

Environmental temperature

Before it was feasible to investigate the effects of temperature on toad body condition, it was first necessary to define the appropriate time of year at which to measure it. This was defined as the month preceding the 'notional' start of the breeding period each year, which was taken as the date on which toad spawn was first found. A period of one month was chosen because, in the absence of equivalent physiological studies in the common toad, it corresponds to the period in the common frog (Rana temporaria) when significant weight loss is known to occur (Ryser 1989). For this analysis, the mean temperature of the pre-spawning period (mT.Sp-1) was determined for each year (1983-93).

With the exception of 1991, the body condition of males was lowest when the mean temperature of the pre-spawning period was high and vice versa (Figure 64). The very low body condition of toads in 1991 compared with other years presents an anomaly that cannot be satisfactorily explained when considered solely in terms of the mean temperature of the pre-spawning month. However, further analysis of the weather data for the preceding year reveals that 1990 was exceptionally dry between March and September. It is, therefore, likely that during this period both food availability and toad foraging activity were reduced, resulting in toads entering hibernation in poor condition. After removing the large influence exerted by the outlying data points for 1991, a regression analysis was done and revealed a significant negative relationship in which 37-49% of the observed variation in male body condition was explained by variation in the temperature of the pre-spawning period. A similar pattern, explaining 25-66% of the observed variation in body condition, was found for females.

Density and environmental temperature

No correlation was found between toad density and the temperature of the prespawning period, and so a multiple regression analysis was used to determine how much of the observed variation in toad body condition could be separately Table 11. Multiple regression analysis of toad body condition against estimated toad density and the mean temperature of the prespawning period in each of four categories of common toad for the period 1980–89. R[≠]=overall proportion of variation explained

Foad group (condition)	Density (p)	Temp/ month (p)	Df	R² (%)	Overall (p)
)-yr male	0.104	0.067	4	82.3	0.031
>0-yr male	0.037	0.084	4	86.6	0.018
)-yr female	0.014	0.004	4	95.9	0.002
>0-yr female	0.198	0.807	4	46.2	0.289

explained by each of the two variables. With the exception of >0-yr females, the effects on condition were either significant or just non-significant at the 5% level (Table 11). In view of the very small number of degrees of freedom (4), these relatively high partial correlation coefficients strongly suggest a separate influence of these two variables on toad body condition, an effect that is likely to be enhanced by the inclusion of additional data in future years.

During recent years there has been an increasing awareness, worldwide, of changes in the status of amphibian populations. These changes have not been consistent, demonstrating increases (eq marine toad (Bufo marinus)), declines (eq cascade frog (Rana cascadae)) and even the extinction of some species (eg gastric brooding frog (Rheobatrachus silus)). Numerous factors have been suggested to explain these changes, including habitat loss, exploitation, pollution and climate change. Unfortunately, very few long-term studies have been done on amphibian populations and so, with the exception of the possible extinctions, the nature of many of these changes cannot be placed within the context of what may be naturally occurring population fluctuations. This research is an example of one of the few long-term studies of an amphibian anywhere in the world and as such provides an excellent opportunity both to observe long-term changes in population status as they occur and to attempt to understand some of the underlying mechanisms governing these changes.

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Modelling the spatial dynamics of a parasitic butterfly and its ant hosts

(This work was funded partly by the British Council and involved collaboration with the NERC Centre for Population Biology (CPB), Imperial College at Silwood Park)

The caterpillars of all species of large blue butterfly (genus *Maculinea*) live underground inside nests of red ants (genus *Myrmica*) for ten months of the year. All five European species are listed among the world's most endangered Lepidoptera. The only British species, *Maculinea arion*, became extinct nationally in the 1970s, but has been re-established following detailed investigation of its life cycle and habitat requirements by ITE and English Nature.



Plate 48. The site for *Maculinea rebeli* in the Pyrenees, where most of the parameters were measured for the population model

We have shown that the caterpillars of three of the European species of *Maculinea*, including *M. arion*, prey upon ant larvae, whereas the other two species have evolved a more advanced cuckoolike relationship with their ant hosts. Apart from a need for scientific understanding of *Maculinea* to aid their conservation, their fascinating parasitic relationships with ants and restricted local populations make them ideal for studying how species interact.

Plate 47. Adult Maculinea rebeli in the Hautes Alpes, France

In the absence of suitable British populations, we have studied populations of both types of Maculinea in continental Europe. However, we have concentrated our initial modelling studies upon the cuckoo-like species Maculinea rebeli (Plate 47), because it is more amenable to laboratory study. Adult butterflies lay eggs on the flower buds of crossedleaved gentians (Gentiana cruciata) where the young caterpillars soon develop through three instars, feeding on the developing flowers. Immediately after its third moult, a *M. rebeli* caterpillar drops to the ground and awaits discovery by a foraging Myrmica ant, which, mistaking it for an ant larva, carries it back to the nest. If it is not found rapidly, the caterpillar is either eaten by other ants or dies after 36 hours.

Although all *Myrmica* ants will adopt *Maculinea* caterpillars with equal facility, each species of *Maculinea* is a specific parasite of a different species of *Myrmica*. Over the next ten months, the appropriate host ant species will nurture a caterpillar to adulthood, but caterpillars taken into a nest of any other *Myrmica* species eventually die. *M. rebeli* is a specific parasite of *Myrmica schencki* and is itself the specific host of a rare hymenopteran parasitoid, *Ichneumon eumerus* (see Elmes, Thomas & Hochberg 1992).

Once the basic population survival parameters had been obtained by a



Figure 65. Maximum annual reproductive rates (R) (and hence carrying capacity) of M. schencki and other Myrmica colonies along the habitat gradient. Nests in cells with R<1 are always in decline and eventually disband (ie values of R below the horizontal line)

series of field and laboratory studies on populations of *M. rebeli* living in the Hautes Alpes in France, we collaborated with scientists from the Universidad Autónoma de Madrid to investigate one of the largest group of populations of *Maculinea* recorded (total 10⁵–10⁶ butterflies), located in a valley of the Spanish Pyrenees (Plate 48). Michael Hochberg (formerly at CPB) then joined the collaboration to help develop mathematical simulation models to explore further the interactions between populations of *M. rebeli*, its gentian foodplant and *Myrmica* ant hosts, using the parameter estimates derived from the earlier studies.

Initially, we investigated recruitment and survival of the butterfly population at different points in its life cycle by means of a simple model using a series of phenomenological terms based on wellexplored theoretical constructs (Hochberg, Thomas & Elmes 1992). The underlying biology of the ant/butterfly system, together with the main results derived from the model, were discussed in full in the ITE Annual Report for 1991–92 (Elmes, Thomas & Hochberg 1992). The simple model suggested that the interaction is globally stable and that



Figure 66. Stable stochastic equilibrium in the absence of the butterfly

i. Typical equilibrium distribution of ant nests on the 1 ha model site of 30×30 cells

ii. Average ant nest size (in caterpillar equivalents) of *Myrmica schencki* and other *Myrmica* in cells along the habitat gradient

parameters associated with the probability of caterpillars being found by and surviving in a *M. schencki* nest have the most effect.

Field study showed that these parameters relate to the relative spatial densities of the foodplants and host ant nests. The M. *rebeli* site in Spain is on a hillside and is defined spatially by the limits of distribution of the crentian foodplant. This area has a natural temperature and moisture gradient, ranging from warm and dry in upper fields to cool and moist in the lower ones. The gradient has some effect on the distribution of gentian plants and a major effect upon the distribution of Myrmica species. The M. schencki population is centred on the hotter, drier habitat and other Myrmica species (Myrmica sabuleti, M. scabrinodis and M. *rubra*) are centred on the cooler, wetter habitat. There is considerable overlap between M. schencki and other Myrmica species in the intermediate conditions.

We investigated this spatial segregation by developing a new, more stochastically based model, which takes account of spatial distributions by dividing the modelled site into a grid of cells. Each cell had an area of 11 m^2 , which is about the maximum area over which the workers from a large *Myrmica* nest forage, so we made the reasonable assumption that each cell contained, at most, one ant nest. Ant colony growth was assumed to be logistic (in the absence of the butterfly), with colony size (W_{t+1}) in year t+1, given by:

$$W_{t+1} = R W_t / (1 + A W_t)$$

where R is the maximum annual reproductive rate, and A (assumed fixed) is chosen to give realistic maximum carrying capacities, (R-1)/A, for each species. The effect of the environmental gradient upon ant nests was simulated simply by varying the maximum annual reproductive rate R (and hence carrying capacity) of each ant species, associated





Figure 67. Stochastic equilbrium when the butterfly is present

i. Typical equilibrium distribution of ant nests on the 1 ha model site of 30×30 cells

ii. Average number of butterflies produced per *M. schencki* nest in different cells along the habitat gradient

iii. Average nest sizes (in caterpillar equivalents) of *Myrmica schencki* and other *Myrmica* in different cells along the habitat gradient

with every cell. For both host and other *Myrmica* species, R was represented by simple unimodal functions of position along the habitat gradient (Figure 65). The foodplants were distributed among cells with a clumped distribution, with density also a function of habitat type, using parameters estimated from the field studies. In theory, the spatial arrangement of the habitat cells can be set up to describe any real site, but it is particularly apt for the simple linear gradient measured on the Spanish hillside site and described here.

Female butterflies were estimated to lay an average of 120 eggs. These were distributed among the gentians according to egg-clumping parameters measured in the field, while subsequent 'contest' type competition ensured that at most only one caterpillar survived per flower bud (2–100 per gentian plant). The probability of fourth instar caterpillars at a plant being found and adopted into a nest depended upon the existence and size of the colony in the same cell, if one currently existed.

Laboratory experiments have shown that inside the nest competition between caterpillars is also of the 'contest' type, such that regardless of how many are adopted a more or less fixed number are reared according to the colony size. It takes about 50 ant workers to sustain one caterpillar at the expense of rearing about 50 ant brood (Thomas, Elmes & Wardlaw 1993), so that a colony rearing a full complement of caterpillars will rear no new workers in spring. The damage to other Myrmica is about 50% of that done to M. schencki colonies because the caterpillars die before they become full grown when adopted by the 'wrong' host.

The full results and parameter sensitivity studies from this spatial model have been published (Hochberg *et al.* 1994). We found that, after randomly seeding the cells of the model site with ant nests but no butterflies, each ant species



rapidly declines in unsuitable habitats, while in preferred habitats large colonies divide and take over vacant neighbouring cells (both processes being dependent on current colony size). A realistic stable but stochastic equilibrium is soon reached (Figure 66).

On introduction of a single fertilized female butterfly, the *M. rebeli* population first booms and then declines. The average colony size of all *Myrmica* nests is reduced. The greatest impact is on M. schencki whose habitat range becomes restricted (c 270 nests ha⁻¹), while the number of other Myrmica nests slightly increases and the interacting Myrmica community reaches a new stable stochastic equilibrium (Figure 67). Sensitivity analyses were used to assess how the model predictions would change if there were errors in the parameter estimates (which are always expected with field estimates), or if the parameter values were different on other sites. As expected, increasing the potential capacity of M. schencki to rear their own brood causes a proportional increase in butterfly numbers.

Figure 68i suggests that the butterfly population would only be endangered by extinction at very low host plant densities (<300 ha⁻¹). As plant density was then increased, a greater proportion of caterpillars both survived on the plants and were adopted into nests. This resulted in decreases in *Myrmica schencki* nests, but increases in the number of butterflies and slight increases in non-host nests because of less competition from *M. schencki*. Surprisingly, the largest population of the butterfly occurs for intermediate plant densities of 1000–1500 ha⁻¹, which is half the densities found on our main study site. Increasing the plant density further leads to overintense pressure on *M. schencki*, slightly reducing their capacity to rear butterflies. This indirect negative effect of the gentians on *M. schencki* is an interesting case of 'apparent' competition between plants and animals.

Another interesting result was that the highest butterfly numbers are supported when only 20% of the annual ant production effort of M. schencki can be transformed into butterflies (Figure 68ii). Myrmica queens lay eggs in early summer, of which a proportion $(1-\alpha)$ develop rapidly and do not suffer much competition with the caterpillars. It is the overwintering proportion, α , that suffers from competition with caterpillars. If all its brood were vulnerable, then overexploitation of M. schencki colonies would decrease the stability of the M. rebeli-M. schencki system as most of the site becomes overrun by other Myrmica species.

The general interest in this cellular automaton approach to spatial modelling



Figure 68. Effect of parameter values on the numbers (ha⁻¹) of adult butterflies, nests of *M. schencki*, and nests of other *Myrmica*. Each point is the mean of the last 50 of 200 generations (usually once stability is reached). Arrows correspond to parameter values used in the study

- i. Plant density (nos ha⁻¹)
- ii. Proportion (α) of annual ant brood vulnerable to competition from caterpillars

of species interactions within a heterogeneous environment is increasing (Colasanti & Grime 1993). However, such spatial models do require difficult field estimation of new types of parameters representing species dispersal, spread and colonisation. Our modelling has highlighted the need for better estimation of colony size-dependent rates of ant nest abandonment and take-over, and of ant nest capacity as a function of habitat type. These are difficult aspects of ant population biology that have been neglected in the past.

We are currently investigating the effect of varying degrees of habitat pattern and fragmentation on the system. Preliminary validation of the model on sites in France, using only local parameter estimates of the habitat and gentian distribution, suggests that this spatial model may adequately represent the subtle general interactions of the butterfly with its plant and ant hosts. It should, therefore, be useful for assessing the effects of habitat manipulation, such as changing grazing intensity or adding/removing host plants. At present, the model does not include annual climatic variation, but in future investigations we can simulate this and even a trend in climate, by permitting annual variation in the position of the habitat gradient (hot dry to cooler damp) relative to the site. This type of spatial mechanistic model should aid our understanding of complex systems of interacting species.

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Long-term scrub succession deflected by fallow deer at Castor Hanglands National Nature Reserve

(This work was funded by English Nature)

Long-term studies of scrub succession at Castor Hanglands NNR. near Peterborough, showed that plots cleared of secondary woodland did not progress to scrub as expected because of fallow deer (Dama dama) browsing on the young woody plants. The original objective of the rotational management of the seral scrub was to provide communities of different ages and structures in a series of plots cleared in successive years. However, this objective was not achieved in the expected timescales of about ten years because of deer browsing. This study shows how scrub succession can be deflected by deer, and will help Reserve managers to decide whether deer are likely to cause similar problems to seral scrub communities elsewhere.

Since 1975, successional changes following clearance of old dense scrub (c 30 years of age in 1974) have been recorded in 12 sequential plots. One plot of 50 m \times 50 m was cleared every year from 1974 to 1985. There were three different initial management treatments. The first four plots were mowed in July and September for the first four-years after clearance to reduce the dense regrowth of the scrub. However, this treatment was also found to jeopardise any future rotational management by preventing seeding from the fine display of early successional plants which appear after clearance (Ward 1990). A second series of four plots was, therefore, mowed in July only for four years. The last four plots were left untreated as the



Figure 69. Average height (cm) of all the woody plants in the three management treatments and the deer exclosure in the years since clearance of original secondary woodland and scrub

effect of deer browsing became apparent. A deer exclosure was set up alongside the untreated plot cleared in 1984.

All plots have four random permanent belt transects of $0.5 \text{ m} \times 25 \text{ m}$, one in each quadrant. All woody plant individuals in the transects were recorded in July every year for three years, and then every other year, by searching through each metre of vegetation; seedlings and regrowth were distinguished and heights measured. Damage by deer browsing on all woody plants was recorded from 1989 to 1993.

In 1993 estimates of fallow deer numbers were obtained by dung counting in July during the growing season of woody vegetation, and in November during the rutting season when deer numbers were expected to be high. Diagonal transects (2 m wide) between the four corners of each plot were cleared of dung and then reassessed seven days later. Repeating the counts immediately indicated that all dung had been located and cleared. Fresh dung that had been marked outside the transects persisted for seven days. Dung of muntjac (Muntiacus reevesi) and lagomorphs was relatively uncommon on the plots. Dung data were converted to estimates of deer days per plot per week using figures for defecation rate from Bailey and Putman (1981) and Stubbe and Goretzki (1991).

This report concentrates on the effects of deer damage on the growth of the shrubs and trees. Other plants were also damaged, particularly flower heads of taller herbs like hogweed (*Heracleum sphondylium*) or great willowherb (*Epilobium hirsutum*), but this did not



Plate 49. Tall grasses and scattered bushes in 1993 nine years after clearance of the unmanaged browsed plot immediately adjacent to the deer exclosure (Transect 12B)

affect seral change to scrub. The important background of population changes of woody plants, and of the interactions between the woody plants and the dominants of the field layer at different stages during the succession is mentioned only briefly.

The average height of all the woody species for each of the three treatment types, as compared to those in the exclosure, shows how deer browsing had suppressed the growth of the scrub (Figure 69). After nine years the average height of the plants in the unbrowsed deer exclosure had reached over 2 m, while it was under 60 cm on all the other browsed plots. Even 12–15 years after the July and September cutting treatments, the average height of woody plants in these plots had not reached 75 cm, and large areas of the plots were still grassland. There were also differences between the browsed plots related to their management, as shown by an analysis of variance of the heights



Plate 50. Closed canopy scrub in the deer exclosure in 1993 nine years after clearance (NB transect marker which is 2 m tall)





reached seven years after clearance. The average vegetation height on the untreated plots was significantly greater than that on both the twice mown (t=6.05; df=6; P<0.001) and once mown plots (t=3.5; df=6; P=0.011). The twice and once mown plots did not differ significantly (t=-1.88; df=6; P=0.11).

The total numbers of plants in the browsed plots after seven years were not significantly different between the management treatments.

The very marked difference in average height of woody plants in the deer exclosure is shown by direct comparison





with the adjacent plot cleared at the same time in 1985. Even after one year there was a small difference. By 1993 the untreated browsed plot gave the general appearance of coarse grassland with scattered bushes (Plate 49), while the deer exclosure had a fully closed scrub canopy with no open areas (Plate 50). The percentage of plants in each height class, five and nine years after clearance, shows how the great majority of plants on the browsed plot were continually suppressed in comparison to the deer exclosure (Figure 70). In the fifth year there were no plants over 80 cm high and even by the ninth year less than 20% were over 1 m high. The decrease in total plant numbers was also greater on the browsed plots (71% as compared to 49%). In 1993, when the tallest plants in the unbrowsed plot were over 3 m, the competition between individuals which occurs as the canopy closes in advancing scrub was just beginning, and shorter individuals were suppressed or dying.

Deer browse woody plants that are easily accessible. The total numbers of all woody plants on all the browsed plots combined over the last five years of the study in each height class, and the percentage of these browsed, are shown in Figure 71. Short plants (10-30 cm) were less browsed, as they were hidden among the very tall dominant grasses (mainly tufted hair-grass (Deschampsia cespitosa) and wood small-reed (Calamagrostis epigejos)). Most of the browsing was at heights of 40-100 cm. The crown of some plants may become progressively wider, and eventually the centre becomes inaccessible and grows

Table 12. Overall percentage browsing on the woody plant species, 1989–93 (includes only species with more than ten individuals)

Species	Nos of plants	Overall % browsed
Prunus spinosa	1360	48
Ulex europaeus	202	41
Cornus sanguinea	772	39
Crataegus monogyna	325	34
Acer campestre	105	30
Rosa spp.	272	27
Rubus fruticosus	2225	25
Sambucus nigra	121	23
Quercus robur	28	18
Rhamnus catharticus	28	14
Euonymus europaeus	40	12
Fraxinus excelsior	125	11
Rubus caesius	631	6
All species	6272	27

Table 13 Fallow deer dung and activity in July and November 1993

Month	Mean <u>+</u> SE dung pellet groups * per 100 m ² per week (i)	Mean <u>+</u> SE deer days per plot per week (11)		Mean <u>+</u> SE deer flushed per plot per visit
July November	$\begin{array}{c} 1 7 \pm 0 3 \\ 2 7 \pm 0 3 \end{array}$	41 <u>+</u> 08 65 <u>+</u> 08	18±04 29±03	$\begin{array}{c} 0 \ 3 \ \pm \ 0 \ 2 \\ 0 \ 2 \ \pm \ 0 \ 1 \end{array}$

* At least eight pellets within 5 cm

Using defecation rate from (1) Bailey & Putman (1981) or (11) Stubbe & Goretzki (1991)

unchecked Other plants are nursed by thick brambles (*Rubus fruticosus*) or gorse (*Ulex europaeus*) and escape from browsing The taller plants were out of reach of deer but may be browsed at the base In fact, most of the larger trees and shrubs at Castor had a browse line with relatively few leaves or shoots below deer browsing height (*c* 140 cm)

Some woody plants are more vulnerable to browsing damage than others (Table 12) Blackthorn (Prunus spinosa) was most affected - 48% of all plants observed from 1989 to 1993 This finding is incompatible with one of the objectives of scrub management at Castor Hanglands, as blackthorn is the host of the rare black hairstreak butterfly (Strymonidia pruni) The scrub plots were intended to supply additional habitat to the over-mature scrub with older dying blackthorn The continual pressure of browsing damage was killing blackthorn, sometimes indirectly of subsequent failure to compete with the taller grasses Dewberry (Rubus caesius) was less affected, with only 6% of plants damaged However, for a full comparison, the height spectrum of all the plants needs to be taken into account Thus, blackthorn was severely browsed at all heights above 20 cm, with as much as 70% grazed at 80 cm (Figure 71) Blackberry (Rubus *fruticosus* agg) was browsed to a much lesser extent at all heights, even at 70-80 cm there was <40% damage Some of these plants had very thorny fast-growing shoots (up to 2 m), and many shoots die annually, leaving thorny thickets which nurse vulnerable species like blackthorm or dogwood (Comus sanguinea) Dewberry is a very much shorter species with weak prickles, and has been increasing vegetatively among the tall grasses on the older plots However, even the taller plants were not browsed as heavily as blackthorn

The scrub rotational management plots make an ideal habitat for deer, with open areas of tall grasses, plenty of browse and bushes surrounded by dense secondary

scrub and woodland in a quiet part of the Reserve Overall deer populations are difficult to estimate, but a greater level of activity on the browsed plots was shown by the dung counts (Table 13), and adults and fawns were flushed from the deep grass Deer activity was not significantly greater in November than in July 1993 The amounts of dung on individual plots in July were not related to the percentage of woody plots browsed on the six plots recorded in 1993 However, when the percentage of plants browsed on individual plots for 1989-93 was summed (range 9-40%), these data were positively related to the sum of dung counted in July and November 1993 (Spearman rank correlation coefficient=0 64, P<0 05)

At Castor Hanglands NNR deer numbers have been high since the 1960s, and have also caused problems to coppice regrowth (Harns 1981) Damage caused by increasing numbers of deer of various species, including the introduced muntjac, is now more frequently noted in nature reserves in southern England Coppice woodland is known to be affected and hence studied (Putman 1994), but, as this study demonstrates, the influence of deer can also be recognised in areas managed for shrubland succession

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