Hares and Skylarks as Indicators of Environmentally Sensitive Farming on the South Downs

Thesis

A Thesis presented to the Open University for the Degree of Doctor of Philosophy, Faculty of Technology

November 1994

Hares and skylarks as indicators of environmentally sensitive farming on the South Downs

Andrew Wakeham-Dawson

Date of submission: 9 November 1994
Date of award: 24 April 1995

Abstract

Grants to farmers are increasingly being directed towards encouraging environmentally sensitive farming practices. This is particularly true in areas that are valued for their landscape and wildlife, such as the chalk grasslands of the South Downs. If such grants are to maintain and improve environmental conditions that are suitable for wildlife, the outcomes need to be monitored regularly. Ideally the form of monitoring should be simple and inexpensive to carry out, to allow farmers to assess for themselves their farms' suitability for wildlife and amend their farming practices accordingly. The current research identified and investigated the potential of hares and skylarks, two easily identified wildlife species which are typical of chalk grassland habitats, as indicators of the quality of farmland for wildlife on the South Downs. Hares and skylarks are familiar species to most farmers and there is some concern among conservationists that the numbers of both species are declining.

The research has shown that both species can be counted without much difficulty. Hare numbers are highest on farms where fox control is practised, and this can over-ride the effects of other factors. When the effect of predator control is allowed for in the analysis, hares appear to favour farms where there is a wide diversity of habitat types. The breeding density of skylarks is determined by more localised environmental factors on areas of farms, such as vegetation height and grazing pressure. Both hares and skylarks can benefit from the introduction of rotational set-aside, but ESA grassland is not favoured by hares or skylarks if grazed very short.

The research suggests that monitoring hares and skylarks could be a valuable aid in assessing the effects of environmentally sensitive farming policy on downland wildlife.

Hares and skylarks as indicators of environmentally sensitive farming on the South Downs

List of contents Page

List of Figures **Page**

List of Tables **Page**

Acknowledgements

Grateful thanks are due to:

Dr Susan Carr, Dr Dick Morris and Dr Stephen Tapper for their inspiration and supervision.

The farmers, landowners, gamekeepers and many others without whose interest and help this research would not have been possible, especially:

Brian Harris, Chris Passmore, David Cross, David Robinson, David West, Dick Passmore, Dr David Brooks, Gerald West, Harry Goring, Ian Currie, John Robinson, Justin and Susan Harmer, Kevin Heath, Mark Ansell, Michael Langmead, Sheila Colman, Nigel Jarvis, Paul and Joan Wakeham-Dawson, Peter Nye, Plumpton Agricultural College, Stan Harvey and Sons, Ted Ray, the late Frank Grantham, the late George Heynes, the Rea family, Tim Carnaghan, and Wayne O'Brien;

Dr Nicholas Aebischer for his comments on the statistical analysis;

My friends at the North-East Surrey College of Technology, especially Dr Ann Bartlett, Dr Susan Easmon, Dr Martin Kurowski, Dr Woi Piotrowski, Mr Dylan Rosser, Mr Fernando Serras, Dr Ruth Shinebaum, Mr Paul Spurdens and Dr Andy Theodorou;

Victoria Haigh and Dick Passmore for the information in Fig 1.1.

Hares and Skylarks as Indicators of Environmentally-sensitive Farming on the South Downs.

General introduction

The arable ecosystem in Britain has been subjected to many different farming practices over the centuries. To a great extent, periodic changes have been initiated by technological advances, and by social and political pressures on the rural community. The most recent changes result from attempts to reform the European Union's Common Agricultural Policy (CAP). European Union (EU) budgeting constraints have lead to a revision of the financial support provided to farmers. The overall objective has been to cut-back the production of commodities in surplus and to reduce the cost of intervention payments. Support is now conditional on agreement by farmers to 'set-aside' land, that is, take it out of production. Unlike previous financial support for agriculture, these reforms have been introduced at a time when public concerns about the loss of wildlife habitat, declines in wildlife populations and over exploitation of natural resources (among many other concerns about the environment) are beginning to have political implications. There is now an increasing trend for new support schemes to attempt to satisfy the interests of both agriculturalists and conservationists.

Although the set-aside schemes as originally introduced had potential environmental benefits, they were primarily designed only to reduce production. In response to the increased concern about the environment, the EU introduced an environmental component to its reforms. This was to be implemented as thought fit by individual governments. In the UK it allowed Environmentally Sensitive Areas (ESAs) to be introduced. Five first round ESAs where designated during 1987 in areas important to agriculture and conservation. These included the South Downs, the Norfolk broads, the Pennine Dales, the Somerset Levels and Moors, and West Penwith.

These are voluntary schemes and farmers are paid to farm in a way that the policy makers believe will best conserve the wildlife, historic and landscape interest of each ESA. In the South Downs ESA farmers are paid particularly to conserve areas of existing chalk grassland, and to create new areas of chalk grassland by ceasing arable production.

Without regular feedback conservationists cannot judge the success of grant schemes, nor farmers the effect of modifying their management practices. The broad aim of this research, therefore, was to investigate a simple and inexpensive key indicator species method for monitoring the effectiveness of environmentally sensitive farming practices in the South Downs ESA ecosystem.

Chapter 1 Agriculture and conservation on the South Downs

1.1 The South Downs

The South Downs were selected as an Environmentally Sensitive Area (ESA), and for this research, because of their unique landscape and wildlife. They are a range of chalk hills which runs parallel to the south coast of England, from near Petersfield in Hampshire (where they have their highest point at 275m) to Eastbourne in Sussex. The northern side of the range has a steep scarp slope, while the southern side dips gently towards the sea. This dip slope is characterised by rolling downland and dry valleys (coombes). There are relatively few hedgerows or areas of woodland on the South Downs. Although the range is cut by a number of rivers, free standing water on the hills is restricted to constructed sheep ponds (dewponds). The South Downs have been agriculturally important since prehistoric times.

1.2 History of agriculture

Pre-1945

There is a myth surrounding the extent of grassland that might once have existed on the South Downs, perhaps based on a mis-interpretation of work by authors such as Hudson (1923). There is a popular and incorrect belief that the South Downs were once exclusively covered in grass. In fact, the South Downs have been a cereal ecosystem (Potts & Vickerman, 1974) for over six thousand years. Downland wildlife has adapted to this ecosystem and the downland turf, itself, is a product of human farming activities.

Six thousand years ago, the downs were mostly covered by deciduous woodland (Tittensor, 1979). By the first century AD when the Romans invaded Britain, the Neolithic farmers had felled this native woodland to provide arable and pasture land. The remains (lynchets) of Celtic field systems are common in almost all parts of the South Downs (Curwen, 1930), and there was possibly less woodland at that time than there is at the present (Tittensor, 1980). Evidence that the downs were also extensively cultivated in the Middle ages is provided by Domesday records (King, 1962). Sheep folded on arable crops at night were grazed on areas of permanent grassland during part of the day. By the late Middle Ages these hills were famous for wool production. Close grazing by sheep and wild rabbits, which were introduced by the Normans (Lever, 1977), produced a fine grassland (downland turf) rich in plants and associated invertebrates on the steeper slopes, where the soils were thin.

Since the eighteenth century, the balance between arable land and grassland has shifted periodically. During the Napoleonic War areas of grassland was ploughed up (Sawyer, 1792) to provide cereals for a besieged country. In addition, advances in sheep breeding and husbandry (Walford-Lloyd, 1924) meant that less pasture land was required. After the Repeal of the Corn Laws in 1846, arable farming entered a period of depression. Much of the arable land was left to 'tumble-down' to grassland. Sheep production continued until 1880, when cheap imports of wool and frozen meat from New Zealand ruined the home market. By 1914 sheep numbers had fallen by two thirds (Passmore, 1992). The reduction in grazing allowed scrub to develop on some areas of the downs.

With the outbreak of war in 1914, the grassland was once again ploughed. This period of boom for farmers was followed by a slump in the 1920s. During this period, cheap imports flooded the home market. Cereal prices crashed and arable land was again left to 'tumble-down' to low grade grassland. The sheep industry fared little better than the cereal industry. Scrub encroached on under-grazed grassland. Some areas were even taken out of agricultural production and planted with trees. It has been suggested that many of the areas of important wildlife habitat that currently exist in Britain originated at the time of this general slump (O'Connor and Shrubb, 1986), although downland turf is not a habitat type that benefits from lax management.

During the Second World War large areas of the South Downs, still under 'tumbled-down' grass after the depression of the 1920s and 1930s, were used as a military training area (Passmore, 1992). This grass was of little value to agriculture and certainly not species-rich downland turf (Dick Passmore; Bill Howe, personal communications). Receiving little management during this period, some areas soon reverted to scrub. Areas not used for training were ploughed to provide wheat.

Even poetic authors such as Hudson (1923), whose work may have contributed to the myth that the downs were once completely covered in grass, record that some areas of the South Downs have always been cultivated. For example, Hudson writes 'the downs are nowhere tame, but I seldom care to loiter long in their cultivated parts. It seems better to get away, even from the sight of labouring men and oxen, and of golden corn and laughing bindweed, to walk on the turf'. In addition, Hudson (1923) also recorded 'all the untilled downland is not turf' and included evidence that many areas of this grassland had been cultivated at some time.

Post-1945

Government grants continued to encourage the ploughing of grassland that had commenced during the War. Improved crop varieties and chemical inputs allowed monoculture systems to replace arable rotations (Ibery, 1992). Even agriculturally marginal areas of downland could now produce an economically rewarding yield. Grazing was much reduced on the remaining areas of grassland. These were by now restricted to steeper slopes, where ploughing was impossible. These areas were often so small that fencing them for stock was not practical and they were abandoned to scrub and dominant grass species. Even grazing by wild rabbits was greatly reduced after 1953, when myxomatosis entered Britain (Thomas, 1963; Corbet and Harris, 1991).

In 1973, Britain joined the European Economic Community (EEC), subsequently referred to as the European Community (EC) and more recently as the European Union (EU). Mechanically and chemically intensive agriculture, especially cereal production, was further encouraged by the subsidy supported Common Agricultural Policy (CAP) of the EU. The CAP was extraordinarily successful in terms of increasing agricultural production, but it eventually resulted in over-production of agricultural produce, unmanageable financial demands on the EC's budget and damage to the natural environment.

The environmental effects of this intensive agricultural production have been discussed by Carson (1962), Mellanby (1981), O'Connor and Shrubb (1986), Green (1989), and Sotherton (1992). Effects on the South Downs, in particular, have been studied by Potts and Vickerman (1974). In summary, the high input systems resulted in a direct loss of wildlife habitat and a decline in the quality of the remaining wildlife habitats, especially in terms of food resources available for wildlife. Wildlife habitat, as used here, includes crop types as well as non-agriculturally productive areas.

The traditional farming practices, which had previously created and maintained wildlife habitats, were abandoned or superseded by new methods. Hedgerows and woodland were removed to increase field size, reducing habitat diversity. Changes in timing and intensity of mechanical activities directly killed wildlife or removed the habitat types in which they lived. Increased pesticide use had direct and indirect effects within food chains. New crop varieties, such as oilseed rape, replaced crops that had been more attractive to wildlife.

1.3 Reforming the Common Agricultural Policy

Pressure for reform of the CAP came from three main sources (Binns *et al.*, 1993). First, non-EC countries complained that the EC's protectionist policies were a breach of free trade philosophy. Secondly, the cost of the CAP had risen from £6 billion in 1982 to an estimated £23 billion in 1992. This absorbed about 60% of the total EC budget. Thirdly, there was an increased awareness, especially among the public, of the environmental consequences of chemically and mechanically intensive agriculture.

There were many proposals for reforming CAP. However, in practice reform proved to be very difficult. The reason for this was that the structure of agricultural support was based on social and political needs, as well as the need to generate adequate levels of food production.

After lengthy and acrimonious negotiations in Brussels, a series of initial reforms of the CAP was implemented. The legislation behind these reforms has been reviewed by Potts (1992) and the legislation relevant to ESAs has been reviewed by Haigh (1987). Some changes were made in 1984 with the introduction of milk quotas, but more comprehensive measures were introduced in 1985, and amended in 1987 , with the first attempts at reducing arable production (EEC, 1985; EEC, 1987).

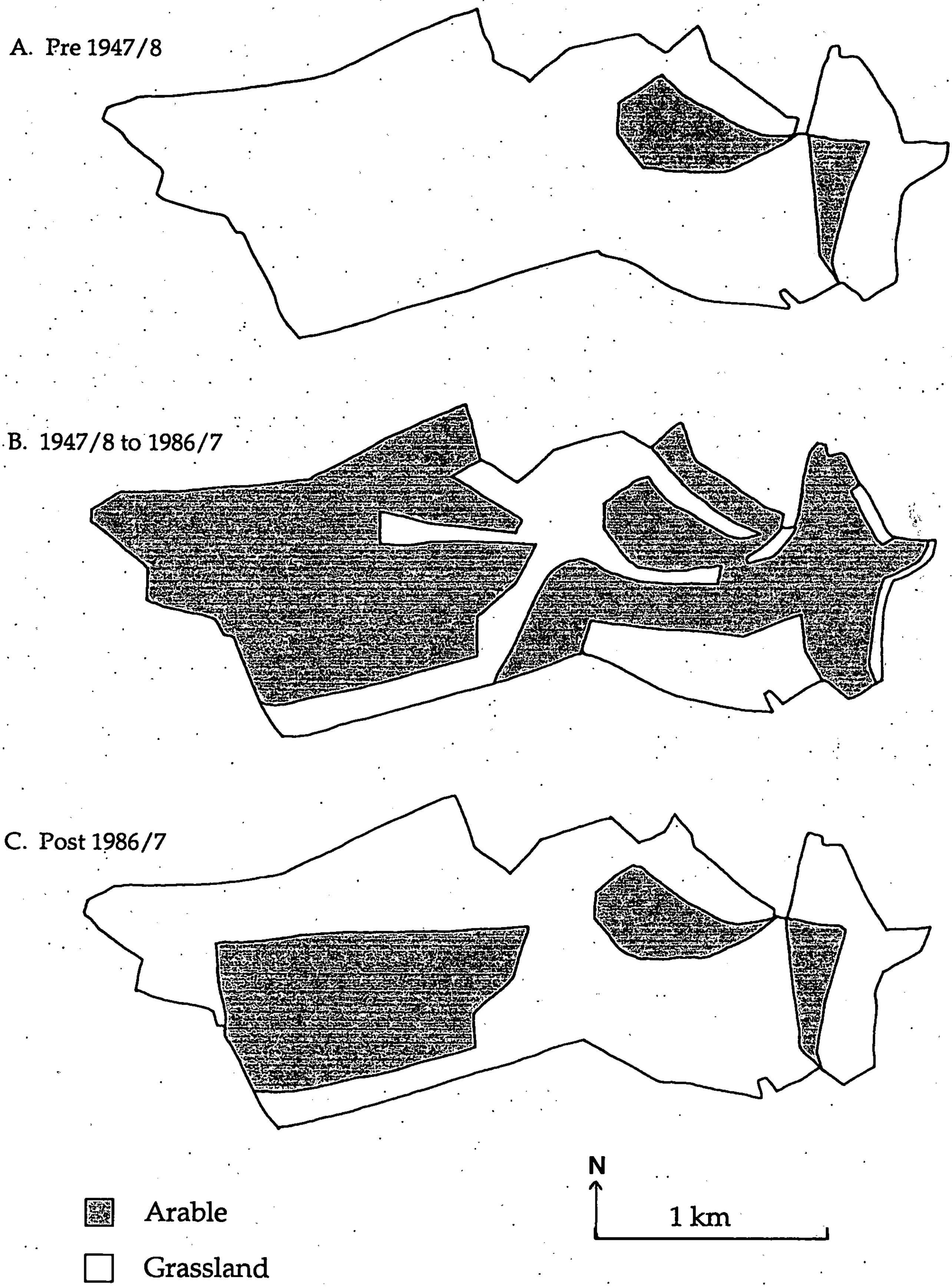
The 'Efficiency of Structures Regulation' (EEC, 1985) also introduced an environmental component into the legislation, by providing national aid for environmentally sensitive areas (Article 19). The EC allowed this environmental component to be implemented as thought fit by individual governments. In the UK, the first five Environmentally Sensitive Areas (ESA), including the South Downs, were designated in 1987. The additional grants available to farmers in the ESAs were designed to encourage traditional farming practices. It was intended that this would safeguard areas of the countryside where the landscape, wildlife or historic interest is of national importance (MAFF, 1994).

In response to the over-production of some agricultural commodities, an EC 'Extensification Regulation' was introduced in 1988 (EEC, 1988). In the UK, this resulted in the introduction of a voluntary set-aside scheme. In order to receive payment under the scheme, farmers taking up the scheme were required to withdraw 20% of their arable land from production and put it into rotational fallow, permanent fallow or woodland for at least five years (MAFF, 1990). However, in 1991, the EC Commission reported that the set-aside scheme had not been effective in reducing arable production (COM/91/100). Consequently, the set-aside scheme was reformed (COM/91/258; COM/91/379). As a result of this, in 1992, there was a reduction in cereal and livestock support subsidies in the UK, and the introduction of compulsory rotational set-aside (15% of the arable production area) for farmers wishing to apply for arable support subsidies (MAFF, 1992a). In 1993, the scheme was further modified to re-include permanent set-aside agreements (MAFF, 1993).

The designation of the South Downs as an ESA has created a new chapter in the grassland/arable cycle. Part of this cycle is illustrated by the changing proportion of grassland to arable on Church Farm, Coombes near Lancing from the 1940s to the 1990s, shown in Fig 1.1. During the Second World War this farm was mostly used as a military training area. After the war, in common with many downland farms, a large area was ploughed for cereal production. After the introduction of the ESA scheme in 1987 much of the farm was returned to grassland.

Figure 1.1

The relative areas of arable and grassland on Church Farm, Coombes since 1947.



1.4 History of conservation

The previous section has summarised the history of reforms to the Common Agricultural Policy (CAP). In 1985, CAP reforms introduced conservation measures as an integral part of agricultural policy for the first time. This represented a radical development in policy making. When the CAP was first established, it did not include any environmental considerations. Conservation on farmland, at this time, relied upon the attitude of individual farmers. While some undertook considerable conservation management, many others were concerned only with agricultural production. By the 1980s, continuing mechanical and chemical intensification of agriculture had become a matter for bitter confrontation between farmers and conservationists (Carr, 1988).

However, agricultural practices were not the only threat to the downland ecosystem. Urban developments spread rapidly along the coastline of Sussex during the first half of this century, threatening to engulf the Downs. It was possibly this threat, rather than concerns about modern agriculture, that prompted the first conservation initiatives on the South Downs.

Whitbread (1993) has outlined the history of conservation on the South Downs. In 1934, West and East Sussex County Councils promoted the South Downs Preservation Bill. This bill failed to receive assent in the House of Lords. In 1947, the Hobhouse Committee recommended the South Downs be given National Park status. However, after the National Parks and Access to the Countryside Act was passed in 1949, and the National Parks

Commission was set up in the 1950s, the South Downs did not receive National Park status. The South Downs were rejected as being too intensively cultivated and no longer sufficiently wild.

Although the South Downs did not received blanket conservation status as a National Park, a number of authorities have acted to conserve some parts of the area: the National Trust (since 1891); the Nature Conservancy Council and its successor English Nature (since 1952); the Sussex Wildlife Trust (since 1961), and East Sussex County Council (since 1971). In addition, the whole area was awarded a degree of blanket conservation status when it was designated as an Area of Outstanding Natural Beauty (AONB) in 1966. Recently a South Downs Conservation Board has been set up by the East and West Sussex County Councils in collaboration with other interested organisations (Whitbread, 1993). The aim is to integrate interested conservation bodies and farmers in a new Downland Strategy based upon the introduction of the ESA scheme.

Until the reform of the CAP, conservation efforts on the South Downs were as fragmented as the areas of wildlife habitat they were designed to manage. The introduction of the South Downs ESA in 1987 has meant that, for the first time, integrated conservation management is being undertaken on both agricultural and non-agricultural wildlife habitats of the downland ecosystem.

1.5 Environmentally sensitive agriculture

1.5.1 Wildlife habitats

In this thesis, each crop or vegetation class is referred to as a wildlife habitat type or, more briefly, habitat type. In its purest sense, translated from Latin, *habitat* means 'it inhabits' and applies to the place or range in which a particular species is found. However contemporary authors often tend to use the word in an imprecise manner. Sometimes *habitat* is used to describe areas that a writer perceives to be suitable for supporting wildlife in general, *ie* wildlife habitat. A second common use of the noun *habitat* is synonymous with 'habitat type'. Here the range of a species may be described as a number of discrete components. For example, hedgerows, pasture and arable crops are all 'habitat types' that occur within the range of brown hares. This is the sense in which the word *habitat* is generally used in this thesis.

Interspersed among arable crops and improved pasture on the South Downs are three other main wildlife habitat types: woodland, scrub in different stages of ecological succession, and downland turf (Henderson, 1979; Page, 1982). Most areas of woodland on the downs are secondary woodland. These are areas of deciduous woodland that have re-established after clearing, or plantations of coniferous or deciduous species, such as Friston Forest near Eastbourne. There are few areas of primary woodland which have escaped ever being cleared. The scrub is composed mainly of deciduous species, especially hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*), and in places, gorse

(*Ulex europaeus*). To the western end of the downs, there are some areas of juniper (*Juniperus communis*) scrub. Detailed citation reports of downland flora present at Sites of Special Scientific Interest (SSSIs) on the South Downs have been prepared by English Nature (NCC, 1986).

Downland turf is a low fertility plagioclimax that has been created and is maintained by the grazing of sheep and wild rabbits. Well managed downland turf is characterised by a closely grazed, compact and species rich sward. There are regional variations in species composition, according to the locality and grazing regime. However, sheep's fescue (*Festuca ovina*) and upright brome (*Bromus erectus*) are often predominant species (NCC, 1986). Downland turf is highly valued by conservationists, and conservation efforts on the South Downs are centred on this habitat type. Its high conservation value stems from (1) its *international* rarity as a habitat type, (2) the wide diversity of plants and associated invertebrates it supports (NCC, 1986), and (3), the fact that many of the species associated with it are on the edge of their range in Europe and unique to this habitat type in Britain.

A Nature Conservancy Council (NCC) survey estimated that less than 6% of the chalk downs in East Sussex were under unimproved downland turf by 1978 (Hendersen, 1979), and showed that most of this was confined to unploughable slopes. The loss of this downland habitat, in common with other habitat types in Britain, has been the combined result of direct habitat displacement and the abandonment of traditional agricultural practices. Downland turf has been (1) ploughed for arable production, (2) replaced by improved grassland (essentially rye-grass species supported by high fertiliser inputs), and (3) replaced by scrub that encroaches as grazing is reduced or abandoned. In this century as in previous times, during periods of boom the downland turf has been ploughed up, and during periods of depression it has been neglected.

1.5.2 The South Downs Environmentally Sensitive Area (ESA)

This voluntary scheme was designed to encourage farmers to re-adopt some of the more traditional farming practices that originally helped create the downland landscape (MAFF, 1994). In particular the scheme was directed at conserving downland turf. Farmers are paid to maintain existing downland turf (Tier 1 agreements), or to convert areas of arable land back into permanent grassland, generally rye-grass (*Lolium perenne*) and white clover (*Trifolium repens*), or chalk grassland, using a seeds mix of chalk grassland species. These last two types of agreement are referred to as Tier 3 agreements. Tier 2 agreements apply only to the river valleys that cut through the downs and these areas were not studied in the current research. ESA agreements are designed to last for a minimum of five years. The detailed management prescriptions for land under these agreements are given in MAFF (1994). In outline the scheme (1) imposes severe restrictions on the use of pesticides and fertilisers, (2) prevents cultivation, (3) prevents 'topping' or mowing before July 16, and (4) limits stocking rates.

In addition to payments for Tier 1 and basic Tier 3 payments, farmers can receive additional payments for using traditional grass seed mixtures on Tier 3 agreements rather than rye-grass and clover seed mixtures, and for maintaining conservation headlands around arable crops. The use of pesticides on these uncultivated headlands is severely restricted.

Potential effects of the ESA on wildlife

The potential benefits of the introduction of the South Downs ESA for wildlife include the following. 1. Prevention of further loss of existing downland turf habitat. 2. Encouragement of the re-establishment of downland grass habitats. 3. Decreased use of pesticides, hence (a) reducing the risk of direct toxic effects on wildlife, and (b) allowing weed and invertebrate populations to re-establish. These species are essential food sources for many species in the downland ecosystem (Sotherton, 1992; Aebischer, 1993). 4. Prevention of hay or silage making until later in the breeding season (after July 16), allowing ground nesting birds to complete their broods. Mowing before this date could destroy nests directly or reveal the young to predators (Poulsen and Sotherton, 1993). 5. Provision of alternative food sources during the summer, when ripening weed-free cereal crops are of low value for herbivorous species such as hares (Tapper and Barnes, 1986).

However, the ESA scheme also has potential disadvantages to wildlife. Potts (1992) suggested that wide acceptance of ESA agreements would 'remove highly diverse parts of the cereal ecosystem' and 'encourage the sowing of fields which have been arable for centuries to rye grass which is valueless to conservation.' Potts (1992) further suggested that the policy makers had not properly considered the ecological requirements of wildlife when designing the scheme. In addition, landowners entering areas in Tier 3 agreements are encouraged to provide new opportunities for the public to walk and pursue quiet recreational activities. This could result in increased disturbance for wildlife.

1.5.3 Rotational set-aside

The downland ecosystem has also been affected by the compulsory set-aside scheme introduced in autumn 1992 (MAFF, 1992a). Under this scheme farmers receiving support grants for arable crops initially had to set aside 15% of their production area as uncultivated fallow. This scheme was modified in 1993 (MAFF, 1993) to include permanent set-aside options in addition to the compulsory 15% rotational fallow that farmers were required to take out of production. Details of management prescriptions for rotational set-aside are given in MAFF, 1993. In summary they are as follows. 1. The set-aside land has to be out of production between 15 December and 15 July of the following year, or between 15 January and 15 August of the following year, depending on the date of harvest. Unlike the case with ESAs, not even grazing is allowed. However, some crops for non-food industrial use can be grown. 2. During the set-aside period a sown or naturally regenerated green cover crop has to be established, but this must be cut short after the 15 July or destroyed with a herbicide or by cultivation by 31 August. 3. Generally, fertilisers and pesticides cannot be applied. However, this was modified in 1993 to allow the use of non-residual, non-selective herbicides for weed control after 15

April. 4. Cultivation or topping for weed control is not allowed until after 1 May.

Potential effects of rotational set-aside on wildlife

The potential effects of rotational set-aside on wildlife are similar to those outlined for ESA grassland. However, while the ESA grassland scheme is likely to reduce wildlife habitat diversity in the arable ecosystem, set-aside is likely to have the opposite effect. On the negative side, if most farmers cultivate or top their set-aside as soon as possible after 1 May, as seems likely, damage will be caused to ground nesting birds in the middle of their breeding season, and plant and invertebrate life-cycles will be disrupted.

1.5.4 Monitoring

Responsibility for monitoring the effects of the ESA scheme on the biology, landscape and socio-economic character of the South Downs fell on MAFF (MAFF, 1991). The biological aspects of this monitoring were designed to 'measure changes in the extent of distribution and quality of wildlife habitats' in the downland ecosystem. In this context, distribution referred only to the area of chalk grassland habitats. Quality was measured only in terms of botanical species richness and diversity.

The first report of monitoring (MAFF, 1991) included the following information on the initial effects of the ESA scheme. This information is included here in detail, because it suggests further ways in which the ESA scheme may affect wildlife.

1. 26% (6048 ha) of the area lying within the South Downs ESA had been placed under agreed ESA management by 1990. Uptake was greater in the eastern end of the ESA. In a few cases farmers placed their whole farm in the ESA scheme.

2. There had been a decrease in the area of scrub on ESA land, compared to surveyed non-ESA land. This will favour steppe species such as hares and ground nesting grassland birds, but will remove nesting habitat for the woodland bird species which have increased in abundance and diversity on the Downs with the encroachment of scrub (Shrubb, 1979).

3. There had been an increase in stocking rates on the ESA grassland. However, this increase many not have been entirely due to ESA management. Data from the 1992 June Census (MAFF, 1992b) indicated a general increase in the national beef herd and sheep flock. Increased grazing pressure will reduce cover for ground nesting birds.

4. It was anticipated that stocking rates on Tier 3 grassland would fall as the productivity of the newly sown grass decreased and nutrient sources became depleted. This will allow less dominant downland plant species to establish, increasing the diversity of plant and associated invertebrates. There is some reported evidence that botanical species richness and botanical species diversity may have increased on agreement land. This increases the range of food species available at the base of downland food chains.

The monitoring scheme appears to be effective in measuring the uptake and success of the ESA in terms of the conservation of downland grassland. However, despite periodic changes in the balance of grassland and arable land since the area was first farmed (as discussed in Chapter 1), the South Downs have been an arable ecosystem since neolithic times, composed of a variety of crop and wildlife habitat types. It is not clear to what extent the replacement of arable land with permanent grassland will affect the ecology of larger wildlife, especially farmland birds and mammals. Current MAFF monitoring does not address this issue.

In future, if policies such as ESAs and set-aside are intended to benefit wildlife, it will be important to follow progress by effective monitoring. Government and conservationists cannot judge the success of grant schemes, nor farmers the effect of modifying their management practices without regular feed back. In addition, to be of practical use, monitoring techniques need to be simple and inexpensive. One possibility is to monitor the impact of these schemes on certain key indicator species, that is species representative of flourishing farmland ecosystems.

1.6 Summary of research objectives

This research had the following specific objectives:

* To develop a method for selecting mammal and bird biological indicator species, that could be used for monitoring the effects of environmentally sensitive farming practices on the downland ecosystem.

* To record the distribution and abundance of the chosen species in relation to farm and farmer characteristics.

* To assess the potential of the chosen species as indicators by monitoring any changes in their distribution and abundance as ESA agreements and rotational set-aside are introduced.

Chapter 2 Selecting indicator species

2.1 Introduction

Chapter 1 summarised the history of agriculture and conservation on the South Downs. It outlined the political and social processes leading to the introduction of support schemes to encourage more environmentally sensitive farming practices. The potential effects of these on downland wildlife, especially mammals and birds, were discussed. The need to monitor the environmental outcomes of such schemes was highlighted. Limitations to the existing monitoring schemes were identified, and the use of biological indicator species as a simple monitoring technique was proposed. In this chapter, a method for selecting mammal and bird indicator species that could be used in a monitoring scheme is developed.

2.2 What are biological indicators?

Biological indicators are organisms whose characteristics provide an indication of some aspect of their environment (Hellawell, 1986; Landres *et al.*, 1988; Soule, 1988). A range of indicator characteristics in a variety of species, including presence or absence, population density, reproductive success, accumulation of substances in body tissues and physiological or behavioural response, have all been used for this purpose. Groups of indicator species at community and ecosystem level have also been used (Hellawell, 1978; 1986).

Some invertebrate species can be used as indicators of chemical pollution, and among these are the earliest examples of biological indicators. For example, one of the first applications of biological indicators was in a study of species composition during the Illinois River Survey (USA) which began in 1877 (Wilhm, 1975). The use of specific organisms as indicators of river pollution was first proposed in 1913 (Wilhm, 1975). The use of pollution indicators has become a more precise science and extended to marine biology (Soule and Kleppel, 1988), and to terrestrial pollution monitoring. A well known example of this last application is the use of lichens as indicators of atmospheric sulphur dioxide pollution (Hawksworth and Rose, 1976).

In addition to their use as measures of specific chemical or physical conditions in an environment, organisms may also be used as an indication of the extent to which an environment is suitable for other species. Plants, invertebrates and vertebrates have been used as indicators to monitor many different environmental conditions. Examples are numerous, but the following are given to show the range of uses to which biological indicators can be put. Butterflies and day-flying moths (Lepidoptera) have been proposed as indicators of the intensity of mowing and chemical use in grasslands in central Switzerland (Erhardt, 1985). The reproductive performance of sea birds has been used to provide information on food resources and thereby indicate the state of a marine ecosystem in the Antarctic (Croxall *et al.*, 1988). Noss (1990) has discussed ways of using biological indicators to monitor changes in biodiversity. Jack pine (*Pinus banksiana*) has been suggested as a possible indicator of global warming (Botkin *et al.*, 1991).

Biological indicators have also been used to assess the perceived scientific or aesthetic conservation value of areas, especially when their potential as nature reserves is being considered. Peterken (1974) used selected groups of woodland plants as a quick method for distinguishing between primary and secondary woodland. Helliwell (1978) used the rarer plant and bird species on farmland to assess the conservation value of areas. Others have used biological indicators to assess and rank wildlife conservation potential of natural areas (Gehlbach, 1975; Goldsmith, 1975; Margules and Usher, 1981).

2.3 Why use biological indicators?

Biological indicators can be used when there is no direct technique available for measuring an environmental condition (Morrison, 1986). They can be employed as an index of attributes too difficult, inconvenient or expensive to measure in other ways (Morrison, 1986; Landres *et al.*, 1988). For example, birds have been used to assess changes in microclimate or insect abundance (Morrison, 1986). Biological indicators can also be used to save time. For example, Peterken's (1974) use of plant indicator groups in a woodland floral survey meant that a detailed census of all species present was unnecessary. In addition, biological indicators allow continuous monitoring of very low levels of contamination (Everett, 1979), such as the accumulation of toxins through a food chain, which might otherwise go undetected (Morrison, 1986). Indicators may have advantages over chemical monitoring in cases where there is a lack of understanding of relationships between chemical criteria and the biological impact of contaminates (British Ecological Society, 1990).

2.4 Overcoming problems with the indicator species concept

However, despite a wide application of the indicator species concept, the use of indicators in scientific study is not without its critics and the reservations of these authors were carefully considered at the outset of the current research. For example, it has been suggested that the use of indicators to determine cause and effect relationships may be misleading (Morrison, 1986; Soule, 1988). In particular, especially in the case of water toxicity tests, that single species response studies are unreliable, because they ignore the complexity of ecosystems (Cairns, 1986). In the case of pollution monitoring, it has been claimed that modern techniques for directly measuring pollution may be more accurate and cost effective (Landres *et al.*, 1988).

Landres *et al.*, (1988) also suggest that the use of indicators of an environment's suitability for other species should be treated with caution. Their arguments are valid, because each species has its own unique ecological niche (Grinnell, 1924; Gause, 1964) and its requirements and responses differ to some extent from any other species. Thus, any attempt to use any one species or even a group of species to perfectly reflect the effects of environmental conditions on other species within an ecosystem would be fatally flawed at the start. This type of flawed philosophy has been referred to as the 'myth of the most sensitive species' (Cairns, 1986). In fact, the use of a few species as indicators in environmental monitoring could be more than just a distracting myth. It could also result, if applied to conservation management, to the protection of a few species at the expense of others (Landres *et al.*, 1988).

Despite their reservations, all these authors were in fact advocating the use of indicators species and were expressing their concerns in order that biological indicators are used only where appropriate and when their limitations are understood. Cairns (1983) even suggested that single species toxicity tests are and would continue to be the 'backbone' of research to determine the effects of toxins on more complex ecosystems.

Soule (1988) outlined some of the considerations that, if kept in mind, allow indicator species to make a valuable contribution to scientific study:

1. There is a 'gap' between indicating a condition and showing cause and effect, or effect and remedy.

2. A single indicator is not a substitute for broad spectrum research or a comprehensive monitoring programme.

3. In-depth knowledge of a single indicator species does not automatically convey information about the way other individuals or species react to environmental conditions.

4. Knowledge about one indicator species does not automatically convey information about interactions between species in communities.

In addition, it has been suggested (Landres *et al.*, 1988) that indicator species, and in particular vertebrate indicators, should only be used when:

1. clearly stated assessment goals have been identified,
2. direct measurements are impossible,

3. the indicators have been chosen by unambiguous and explicit criteria.

2.5 Why biological indicators were used in the present study

The present research is concerned with investigating the effects of existing and newly introduced farming and conservation practices on the mammals and birds of the South Downs. An indicator species approach based upon population density was decided upon as the best way of examining these effects. The first reason for this was that the only way to examine effects of changes in environmental conditions on a species is to study the response of *that* species. However, there are a large number of species within the downland ecosystem. Where would one start? The choice of one or two indicator species whose lifestyle makes them subject to changes in agricultural practice and whose response is probably similar to that of other species would be a good start. In particular, species that use a wide range of wildlife habitats, and by their position in a food chain indicate abundant and diverse floral and invertebrate communities within the downland ecosystem could have potential as indicators for this application. The second reason for choosing an indicator species approach was so that the method could be used by non-specialist researchers. This would allow farmers and other downland managers themselves to monitor the effects of modifying their farming practices. A simple monitoring method based on a number of easily identified indicator species would allow farmers and conservationists a very immediate form of feedback to which they could respond by adjusting their management practices if necessary. Population density changes from a base-line population were proposed, rather than more complex indicator characteristics such as productivity or mortality responses, to keep the method simple and widely applicable.

2.6 What criteria should be used to choose indicator species?

2.6.1 Selection criteria in the literature

A number of criteria for selecting many different types of indicator species for a wide range of research have been described; for example see Hawksworth and Rose, 1976 (lichens, atmospheric pollution monitoring); Hellawell, 1978 (aquatic organisms, water pollution monitoring); Noss, 1990 (terrestrial organisms, biodiversity monitoring); Landres *et al.*, 1988 (vertebrate indicator species selection); Croxall *et al.*, 1988 (marine vertebrates, marine ecosystem quality monitoring); Kremen, 1992 (Lepidoptera, ecosystem disturbance assessment).

The most generally used selection criteria, with the emphasis on those of particular relevance to the aims of this research are outlined and discussed here. The discussion is in terms of vertebrate indicators, regardless of whether the criteria were originally designed for the selection of vertebrates or not.

1. Distribution. Habitat generalists are more useful as general indicators of ecosystem quality for *vertebrates*, as most vertebrate species use a range of habitat types (Landres *et al.*, 1988).

2. Abundance. Abundant species should be chosen as indicators, because this makes sampling easier (Hellawell, 1978; Landres *et al.*, 1988).

3. Identification. Indicator species should be easy to identify and survey (Hellawell, 1978).

4. Response. To be effective, indicators must be sensitive to the environmental contaminates or habitat attributes under study (Landres *et al*., 1988) and show a range of sensitivity to differing levels of stress (Hawksworth & Rose, 1976; Hellawell, 1978).

5. Ecology. The ecology of the chosen species should be well understood, allowing the effects of natural population regulation factors to be differentiated from the impact of the factors being studied (Noss, 1990).

6. Economic status as pests or game. Pest and farmed species should be avoided (Hellawell, 1978) as anthropogenic factors may over-ride other conditions under study.

7. Residency status. Only non-migratory species should be selected as indicators. Otherwise, a change in abundance may be unrelated to the habitat conditions on the breeding ground (Landres *et al*, 1988).

2.6.2 Selection criteria used in the present study

Selection of indicator species for use in the present research followed three stages.

Stage 1. An initial screening process was carried out to identify vertebrate downland species with potential as indicators of the general response of mammal and bird communities to changing farming practices. This was based on nine criteria that were designed for the present study from the review of criteria described in 2.6.1. The nine new criteria were designed to identify downland species (1) whose ecology was well understood, (2) which were not affected by regular population cycles or other factors unconnected from the impact of the factors being studied, (3) which were adapted to agricultural ecosystems, (4) which were habitat generalists, (5) which were abundant, (6) which were not farmed or (7) controlled as a pest, (8) which were easy to study, and (9) which were resident within the study area throughout their lives.

In order to do this the literature on a wide range of downland mammal and bird species was examined, especially that relating to the nine selection criteria just described. From this literature review, 18 species of downland mammal and five species of downland birds were initially selected as possible indicators (Appendix A).

Stage 2. Using literature reviewed in Corbet & Harris (1991) for mammals, and Witherby *et al.* (1938) and Marchant *et al.* (1990) for birds, each of the 18 species of mammals and five species of birds selected in Stage 1 was awarded a relative score based on the degree to which they fulfilled each of the nine criteria that were designed for the present research (from 0, for not at all, to 5, completely). Witherby *et al.*(1938) was chosen as an information source in preference to some more recently published sources. The basic biology of British birds is well described in this work.

Table 2.1 Indicator potential value (IPV) of 18 species of downland mammal (see text for explanation).

	Criterion						
	2	**3**	**4**	**5**	**7**	**8**	**IPV**
Species							
Brown hare	5	5	5.0	3	4	5	27.0
Wood mouse	5	0	5.0	5	4	3	22.0
Hedgehog	5	0	1.5	4	5	3	18.5
Common shrew	0	0	5.0	5	5	3	18.0
Badger	5	0	1.5	3	5	3	17.5
Mole	5	0	5.0	4	0	3	17.0
Rabbit	3	0	5.0	4	0	5	17.0
Pygmy shrew	0	0	4.5	4	5	3	16.5
House mouse	5	0	3.5	4	0	3	15.5
Field vole	0	0	2.0	5	5	3	15.0
Harvest mouse	0	0	5.0	2	5	3	15.0
Bank vole	0	0	1.5	5	5	3	14.5
Fox	5	0	1.5	3	0	5	14.5
Dormouse	5	0	0.5	1	5	1	12.5
Squirrel	5	0	0.5	4	0	3	12.5
Roe deer	5	0	0.5	3	0	3	11.5
Weasel	0	0	1.5	4	0	3	8.5
Stoat	0	0	1.5	3	0	3	7.5

Table 2.2 Indicator potential value (IPV) of five species of downland bird (see text for explanation)

	Criterion						
	3	**4**	**5**	**6**	**8**	**9**	**IPV**
Species							
Skylark	5	3.5	4	5	5	3	25.5
Lapwing	5	3.5	2	5	5	3	23.5
French partridge	5	3.5	2	0	5	5	20.5
Grey partridge	5	3.5	2	0	5	5	20.5
Meadow pipit	0	1.5	3	5	1	5	15.5

Stage 3. These scores were then summed to provide an indicator potential value (IPV) for each of the 18 species of mammal and five species of bird.

The results of the assessment are shown in Table 2.1 for the 18 mammal species and Table 2.2 for the five bird species. The following notes, which are based on the literature review of Stage 2 explain the allocation of scores.

CRITERION 1 (ecology well understood): All 18 species of mammals and five species of birds have been widely studied. Thus in this particular case, criterion 1 had no discriminatory value and was therefore excluded from the calculation of IPV.

CRITERION 2 (fluctuating population): Shrews and voles undergo marked population fluctuations. In voles, these are most marked in northern Europe (Scandinavia) were there are clear multi-annual cycles. Although there is no evidence for multi-annual cycles in Britain, vole numbers fluctuate dramatically (Corbet & Harris, 1991). Stoat and weasel populations undergo fluctuations in response to changes in prey availability (Corbet & Harris, 1991). Harvest mice may also undergo cyclic population fluctuations. All these species were therefore given a score of zero for this criterion. Rabbits are heavily influenced by myxomatosis. This species was awarded a score of 3 for this criterion. A score of 3 rather than 0 was given to rabbits as the influence of myxomatosis was considered to be less influential in their ecology than previously.

None of the other mammal species or bird species show strong evidence of cyclic population fluctuations. These species were awarded 5 for this criterion in Table 2.1. This criterion was excluded from Table 2.2 as it was not discriminatory and therefore did not assist in the allocation of IPV.

CRITERION 3 (adapted to agricultural ecosystems): Hares, skylarks, lapwings and the two partridge species are well adapted to living in regularly cultivated farmland. These species were awarded 5 for this criterion. It is interesting to note at this point that despite the adaptation of these species to agricultural ecosystems, all four species have shown long term population declines over the last 20-30 years. Although all the other species make use of cultivated land to some degree, they require undisturbed areas of woodland, hedgerow or grassland. These species scored zero for this criterion. This criterion did not take into account species that may have adapted to using farm buildings (eg house mouse).

CRITERION 4 (habitat generalists): For this criterion, species that use a wider range of habitat types within the downland ecosystem were considered to have greater indicator potential than those with a more restricted range. Habitat use by the mammal species is shown in Table 2.3. Habitat use by the bird species is shown in Table 2.4. Information for this criterion was drawn from Corbet and Harris (1991) and Whitherby *et al.* (1938). Areas with numeric values in these tables indicate that a habitat is generally used by a species, areas marked 'X' that it is not generally used. The score within the used areas is weighted to represent the relative extent of each habitat type on the South Downs. The relative extent of each habitat type on the

Table 2.3 Habitat types used by 18 species of downland mammal (see text for explanation), Key: A, arable land; G, grassland; S, scrub; W, woodland; H, hedgerow; X, habitat type not used.

	Habitat type				
	A	**G**	**S**	**W**	**H**
Species					
Brown hare	2	1.5	1	0.5	0
Wood mouse	2	1.5	1	0.5	0
Hedgehog	X	X	1	0.5	0
Common shrew	2	1.5	1	0.5	0
Badger	X	X	1	0.5	0
Mole	2	1.5	1	0.5	0
Rabbit	2	1.5	1	0.5	0
Pygmy shrew	2	1.5	1	X	0
House mouse	2	1.5	X	X	0
Field vole	X	1.5	X	0.5	0
Harvest mouse	2	1.5	1	0.5	0
Bank vole	X	X	1	0.5	0
Fox	X	X	1	0.5	0
Dormouse	X	X	X	0.5	0
Squirrel	5	X	X	0.5	X
Roe deer	X	X	X	0.5	X
Weasel	X	X	1	0.5	0
Stoat	X	X	1	0.5	0

Table 2.4 Habitat types used by five species of downland bird (see text for explanation), Key: A, arable land; G, grassland; H, hedgerow; X, habitat type not used.

	Habitat type		
	A	**G**	**H**
Species			
Skylark	2	1.5	X
Lapwing	2	1.5	X
French partridge	2	1.5	0
Grey partridge	2	1.5	0
Meadow pipit	X	1.5	X

South Downs was estimated from detailed habitat maps of the Game Conservancy Trust's Sussex study area (held at Fordingbridge). Thus hedgerows are the most rare downland habitat type and score zero, woodland scores 0.5, scrubland scores 1 and grassland scores 1.5. Arable land is the most common habitat type and scores 2. The sum of these values is the score for this criterion, for example, the brown hare scores 5 on criterion 3 (2 + 1.5 + 1 + 0.5 + 0). Woodland or scrub were excluded from Table 2.4, as the bird species studied do not regularly use either habitat type.

CRITERION 5 (abundance): The relative abundance of each species was based on information in NCC (1989) and backed up by information in Corbet & Harris (1991) and Marchant *et al.* (1990). Abundant species scored 5; very common species 4; common species 3; common, but local, species 2; and uncommon species 1.

CRITERION 6: (not farmed) None of the mammal species is farmed, so this criterion was excluded from Table 2.1. The partridge species are farmed as game, so these species scored zero for this criterion in Table 2.2.

CRITERION 7: (not a pest species) Some of the mammal species (rabbit, fox, stoat, weasel, house mouse, roe deer, grey squirrel and mole) are controlled as pests. As an indication of the very great effect this type of control would have on indicator potential, these species scored zero for this criterion. As brown hares and wood mice occasionally reach pest proportions, these species scored 4 for this criterion. None of the bird species is controlled as a pest, so this criterion was excluded from Table 2.2.

CRITERION 8 (ease of study): The scores for this criterion are based on a review of survey methods. Direct survey methods involving counts of animals were considered easiest to perform. Of the mammals, rabbit, hare and fox populations can be surveyed in this way. Of the birds, partridges, lapwings and skylarks can be similarly surveyed. All these animals scored 5. Those species that are usually surveyed by indirect methods, for example small mammals (by capture, mark, recapture methods), deer (by faecal counts) and badgers (by sett counts) scored 3. Meadow pipits (Marchant *et al.*, 1990) and dormice (Corbet and Harris, 1991) can be difficult to survey and scored zero on this criterion.

CRITERION 9 (resident in the study area): All the mammal species were resident in the study area, so this criterion was excluded from Table 2.1. Lapwings and skylarks, which can be partial migrants, scored 3 on this criterion. All other species in Table 2.2 scored 5.

Summation of scores gave brown hares (*Lepus europaeus*) the highest IPV of the mammals (Table 2.1) and the skylarks (*Alauda arvensis*) the highest IPV of the birds (Table 2.2). These species were therefore the ones selected for further study.

Chapter 3 Farm management practices

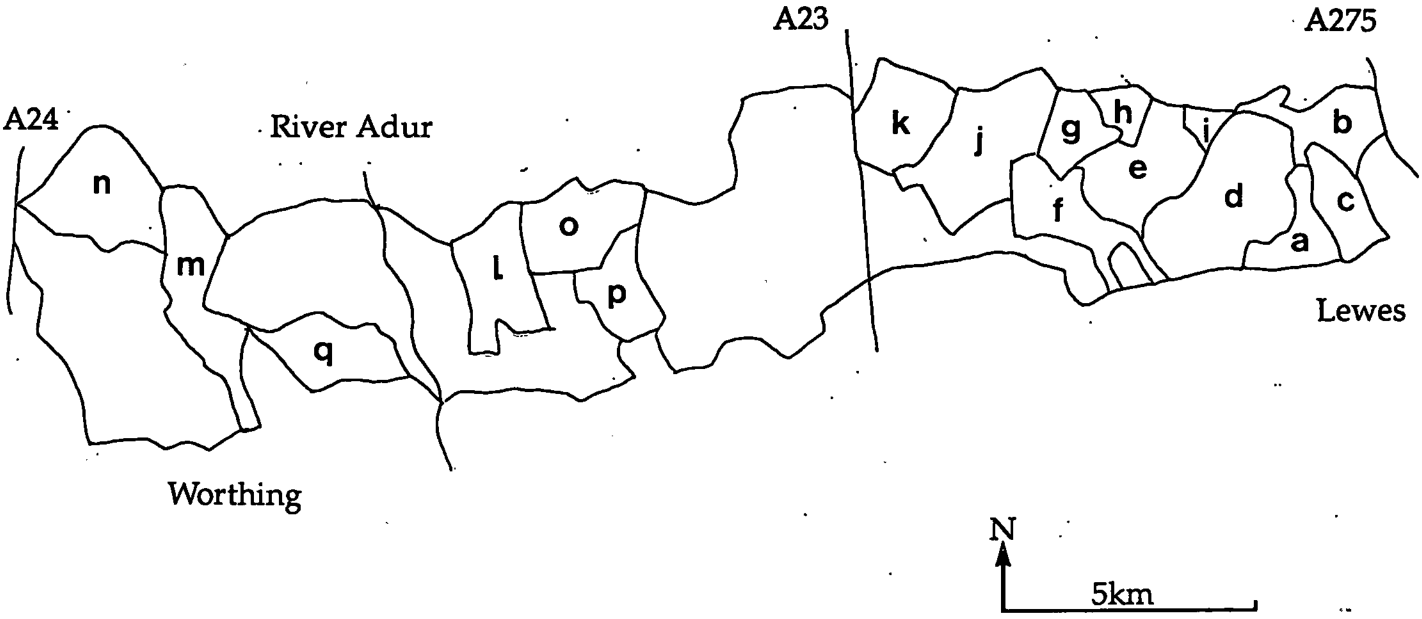
3.1 Introduction:

In Chapter 2 a theoretical method for selecting potential vertebrate indicators for use in simple and inexpensive monitoring of the effects of environmentally sensitive farming practices in a downland ecosystem was developed and applied. Two species, brown hares and skylarks, were chosen for more detailed investigation. The remaining four chapters describe how a practical assessment of these species' indicator potential was made based on the changes in abundance and distribution of both species which followed the introduction of ESA grassland and rotational set-aside. Chapter 3 describes how the study farms were selected, and the farm management practices on these farms investigated. It discusses the changes in farm management policy and environmental conditions that accompanied the new farming practices. This information is then used to help interpret the results of Chapters 4 and 5 which describe an investigation into the response of the hare and skylark populations to these changes. Chapter 6 then draws the results of the current and related research together, and further discusses the indicator potential of hares and skylarks.

3.2 Methods

The practical assessment of the indicator potential of hares and skylarks was carried out on 17 downland farms (a total area

Figure 3.1 The study farms



of 53 km^2) between Lewes and Worthing in Sussex (Fig 3.1) over a three year period. This area was chosen primarily because it provided farms within realistic travelling distance of the research base. The study area included farms which represented the different wildlife habitat types and farming practices that characterise the eastern end of the South Downs. Groups of adjacent farms were selected in an attempt to establish a clear indication of the distribution of hares and skylarks.

Initially, 12 farmers situated between Lewes and the A23 were visited by appointment in autumn 1990 to outline the aims of the project. 11 out of the 12 farmers agreed to participate in the project, some showing considerable interest. The one other farmer also agreed to take part in the project. However, being a particularly precise arable farmer, he was concerned that the hare survey would cause damage to his crops. As a result he imposed restrictions to the survey method and so it was decided that his farm should be excluded from the study.

Where the farmer agreed to allow the survey, some preliminary information was collected at this stage: (1) The farm boundary and current cropping patterns. These were recorded on OS maps. Further information was added to these maps during field walks made during the three years of field investigations. To help classify the types of grassland within the study area, reference was made to a recent survey of chalk grassland on the South Downs (Henderson, 1979; Page, 1982). (2) Brief, informal and unstructured interviews were conducted with the farmers to provide background information about their farm management practices. In addition, the methods that would be used to survey hares and skylarks (see Chapters 4 and 5) were explained.

From the information on cropping patterns and habitat types, the diversity, that is a measure of the range and relative proportions, of the crop types and the vegetation classes present on each farm was estimated using the Shannon-Weiner information measure (Zar, 1984). This procedure was repeated for each of the three years of the study from information recorded on the maps made during the farmer interviews and field walks. The areas of each vegetation or crop type were estimated using a transparent grid which was placed over the maps. The Shannon-Weiner information measure indicates diversity (H) on a scale of 0, for no diversity, to 1, for wide diversity. An estimate of relative diversity (J) can be derived from H, which allows diversity to be compared between areas or years with different numbers of vegetation or crop types (Zar, 1984).

The initial survey showed the diversity of wildlife habitats was very similar on all the chosen farms. As habitat diversity has an important influence on the ecology of hares and skylarks (see Chapter 4 on hares and Chapter 5 on skylarks), it was considered important to include a range of farm habitat diversities in this research. As a result, a further six farms (three between the A23 and the River Adur, and three farms west of the Adur) were included in the study, making a total of 17 farms. Only one farmer approached at this stage did not agree to take part. This farmer was concerned that published data would lead to public interest and interference with the wildlife. This farm was excluded from further study.

More information was collected by means of formal, structured interviews with all 17 farmers in the winter of 1993/1994 (the last year of the study). The basis for the interviews was a questionnaire, which included questions on hares and skylarks, and questions on farm management practices. A copy of the questionnaire is provided in Appendix B. The questionnaire itself was constructed from information collected in the initial unstructured interviews with the farmers, from questions raised from the review of the literature relevant to this research and from preliminary formal interviews conducted with six of the 17 farmers during spring 1992. The questionnaire included questions that were designed to collect information on the farming practices and recent changes in farming practices that would be most likely to affect the ecology of hares and skylarks, such as changes in the diversity of wildlife habitats and food availability. See Chapter 4, on hares, and Chapter 5, on skylarks, for a detailed discussion of the ecological conditions and resources these species require.

Information on farm livestock, collected in the interviews with farmers, was used to calculate stocking density (on each farm where livestock were kept) by a two stage process. First, the number of livestock units on each farm was estimated using the livestock unit values of 0.15 for each sheep and 1.00 for each beef or dairy cow as given in MAFF (1994). Then the number of livestock units on each farm was divided by the area of grassland on each farm.

3.3 Results

3.3.1 Farm enterprises

The means of information collection described above revealed that of the 17 study farms, four were arable farms, ten mixed arable/livestock farms (including four dairy farms), and that the total area of the remaining three farms had been entered into the ESA scheme. This meant that livestock were kept on the last three farms, but that arable enterprises were not allowed under the terms of the ESA agreement (Table 3.1). Game birds were reared on six of the 17 farms. On four of these a professional gamekeeper was employed, on the remaining two the farmers did their own game management.

3.3.2 Pesticide use

The intensity of pesticide use was assessed by comparing the types and applications of chemicals that farmers were using on winter wheat (Table 3.1). High users were categorised as those who used a wide range of products, and frequent and prophylactic applications. Medium users were categorised as those who generally treated the crop only when a problem occurred, but used a wide range of products and a number of applications. Low users were categorised as those who only used the essential minimum of pesticides. Farms in the high category tended to be arable only, those in the medium and low categories tended to have a mixture of arable and livestock.

Table 3.1 Summary of management practices on study farms. MA = mixed arable/livestock; A = arable only; D = dairy; ESA = whole farm entered in permanent ESA grassland. H = high; M = medium; L = low.

Farm	Type	Pesticide use	Fertiliser use:grass	Fertiliser use:arable
A	MA	M/H	L	M/H
B	MA	L	L	L
C	A	H	-	H
D	MA/D	M	H (dairy)	M
E	A	H	-	H
F	MA/D	M	H (dairy)	M
G	MA	L	none	L
H	A	M/H	L	M/H
I	MA	M	L	M
J	ESA	none	none	-
K	MA	L	L	M
L	ESA	none	none	-
M	A	H	-	H
N	MA/D	M/H	H (dairy)	M/H
O	ESA	none	none	-
P	MA/D	M	H	M
Q	MA	M/L	none	L

Pesticide use on ESA grassland is against regulations, with a very few exceptions (such as thistle control). As a result pesticide use on ESA grassland was negligible.

Generally farmers in the low use category were motivated by a need to keep costs down, rather than by concerns about the toxic effects of pesticides. Most farmers in the high use category justified intensive spraying on the grounds that they were in business and wished to stay in it. However, it was difficult to generalise from pesticide use on one crop the use on the farm as a whole. Most farmers had different policies for different crops on their farms. For example, one farmer used moderate applications of pesticides on wheat, but very little, if any, on conservation grade oat crops. Only two farmers had unsprayed conservation headlands on their farms, but were in the low pesticide use category anyway. One medium/high pesticide user was in the process of trying out conservation headlands. One of the high pesticide use farmers had tried conservation headlands and abandoned them as creating a weed problem. Conservation headlands are an important source of weed and invertebrate food for wildlife (Sotherton, 1992) and therefore it was important to consider the effects of their presence in the current research.

3.3.3 Fertiliser use

Intensity of fertiliser use was assessed by investigating the annual applications of artificial nitrogenous fertilisers made to winter wheat crops and to all types of grassland. The intensity of fertiliser application was categorised according to the farmers' own descriptions of their usage, but as a guide (given to the farmers at time of interview), high application exceeded 250 kg/ha/year, medium use was in the 100-250 kg/ha/year range, low use did not exceed 100 kg/ha/year (Table 3.1). The exclusively arable farmers all used large amounts of nitrogen on their winter wheat. Mixed arable/livestock farmers tended to use only moderate applications of nitrogen on all crops, including wheat.

Only dairy farmers applied large quantities of nitrogen to grassland, and only to the dairy grazing and silage grass. Like other farmers they applied low levels of nitrogen to other categories of grassland. It is against MAFF regulations to apply nitrogen or any other type of fertiliser to ESA grassland.

3.3.4 Livestock and stocking density

Although an attempt was made at estimating stocking density (Section 3.1, Table 3.2), it is difficult to tell just how representative the calculated value is of the grazing pressure on the study farms. The reason for this is that some farmers kept sheep on their farms only during the winters, while other types of stock (dairy cows and some beef herds) were housed during this period. On farms with large areas of ESA grassland, stocking density was low, and the animals tended to roam freely over the whole area. On other farms, including dairy farms, stocking density was higher, but leys and pastures were grazed in rotation. This meant that these areas were stock free for some periods.

Table 3.2 Summary of management practices on study farms, showing livestock numbers, hay making (date of cutting) and silage making (number of cuts; first cuts around 10 May, second and third cuts in July, August or September). MA = mixed arable/livestock; A = arable only; D = dairy; ESA = whole farm entered in permanent ESA grassland. H = high; M = medium; L = low. S = sheep; B = beef; C = dairy cows. SD = stocking density (livestock units/ha).

* (in livestock column) = information as given by farmer.

Farm	Type	Livestock	SD	Hay making	Silage making
A	MA	400s,100b	5.5	June	no
B	MA	500s,177b	2.4	June/July	1 (July)
1C	A	-	-	-	-
D	MA/D	350s,350b,150c	2.7	no	1 (May)
E	A	-	-	-	-
F	MA/D	250b,120c	4.0	July	3
G	MA	60b	3.2	July	no
H	A	-	-	-	-
I	MA	?s	-	no	no
J	ESA	?s	-	July	1 (July)
K	MA	1200s	2.7	late June	no
L	ESA	2.5s/acre*	0.9	July	no
M	A	-	-	-	-
N	MA/D	?c,?s	-	July	3
O	ESA	2.5s/acre*	0.9	July	no
P	MA/D	30b,113c	1.6	no	3
Q	MA	1.4lu/ha*	1.4 -	June	no

3.3.5 Hay and silage making

Only the dairy farmers made more than one cut of silage. The first cut tended to be in May, the second in July and the third in late August or in September (Table 3.2). Other farmers made only late cuts of silage or hay in June or July. Under MAFF regulations, hay or silage cannot be made on ESA grassland until after July 16.

3.3.6 Wildlife conservation

All farmers reported that they had species of interest on their farms and that they were taking part in one or more of a range of conservation activities to encourage wildlife. Organisations from which they had taken advice included MAFF (ADAS), the Country Landowners Association (CLA), the Farming and Wildlife Advisory Group (FWAG) and the Game Conservancy. Most farmers considered that taking part in the ESA scheme was a contribution towards conservation, but very few of them felt that the scheme in its current form was of any benefit to wildlife. One farmer described a large area of ESA grassland on his farm as a wildlife desert. Conservation projects described included the improvement of access to barns for barn owls, hedge laying, woodland coppicing and maintenance of dew ponds (Table 3.3). Farmers who managed their land for gamebirds were particularly active in maintenance of scrub and wooded areas as coverts. They also planted areas of game cover crops which provide food for gamebirds and other wildlife species in the winter.

3.3.7 Rotational set-aside

The rotational set-aside scheme was introduced in the autumn of 1992. Over the following Winter 1992/1993, ten of the study farms had rotational set-aside within the study area. Over all, rotational set-aside at this time covered 362ha, approximately 7% of the total study area. After May 1 (when the EC legislation allowed rotational set-aside to be managed for weed control) seven of the farmers opted to cultivate their set-aside (a total area of 288 ha), while three decided to top the vegetation (a total area of 74ha), Appendix C1c. The area of stubble remaining over the winter in the study area increased from 503 ha (9.4% of the total area) in 1991/1992 to 626 ha (11.8% of the total area) in 1992/1993.

Downland farmers generally tend not to leave fields as a stubble fallow over the winter. They usually plough in the autumn and sow winter crops or leave the field as plough until spring sowing. The introduction of the rotational set-aside scheme caused the area of stubble left over this period to increase, thus providing additional feeding areas for wildlife over the winter.

In the second year of rotational set-aside (1993/1994) the area of stubbles left over the winter was 11.3%, an area similar to that in 1992/1993.

3.3.8 ESA grassland

The ESA grassland scheme was introduced in 1987. By the first winter of the present study, in 1991/1992, 11 of the study farms had at least some grassland in ESA. A further two farms had their whole area entered in the ESA scheme. Overall, grassland covered 1,820 ha, approximately 34% of the total study area. Just under 80% (1426ha) of this area of grassland was entered in the ESA scheme (Table 3.3).

By the second winter of the study in 1992/1993, the area of grassland in the study area had increased by 6% to 2116 ha (40% of the total study area). This was the result of a continued uptake of small scale ESA grassland agreements by several of the study area farmers. In addition, the entire area of one more mixed/arable farm (394ha) was entered in the ESA scheme during this period. At this time two of the farms were withdrawn from the ESA scheme, because of a disagreement over payment. By the third winter of the study, in winter 1993/1994, the area of grassland in the study area had not changed since the previous winter.

3.3.9 Wildlife habitat diversity

Relative habitat diversity was estimated for each farm during December/January of each of the three winter periods, using the Shannon-Weiner method described in Section 3.1. Habitat diversity values can be found in Appendix D. The winter habitat diversity in 1991/1992 was compared with the spring/summer

Table 3.3 Summary of management practices on study farms, showing conservation activity and management of rotational set-aside. MA = mixed arable/livestock; A = arable only; D = dairy; ESA = whole farm entered in permanent ESA grassland; ESA* = some grassland in ESA scheme; ESA** = all grassland removed from ESA scheme after Winter 1992/1993; SC = scrub clearance, HL = hedge laying, C = coppicing, DP = dew pond construction; Topped = rotational set-aside topped for weed control after May 1; Cult = rotational set-aside cultivated for weed control after May 1.

Farm	Type	Conservation activity	Set-aside management
A	MA	ESA**	-
B	MA	ESA*, SC	-
C	A	-	cult
D	MA/D	ESA*, SC	cult
E	A	-	-
F	MA/D	-	-
G	MA	ESA*, SC, HL, C	cult
H	A	ESA**	cult
I	MA	ESA*, SC, C	topped
J	ESA	ESA*, TP, HL, C	-
K	MA	ESA*, SC, CH, DP	cult
L	ESA	ESA*	-
M	A	-	topped
N	MA/D	ESA*, SC, HL	topped
O	ESA	ESA*	-
P	MA/D	ESA*	cult
Q	MA	ESA*	cult

habitat diversity in 1992. As there was no significant difference (Appendix D2), the habitat diversities estimated in the winter periods were used as an indication of habitat diversity throughout the year. Habitat diversity was wider on mixed livestock/arable farms than on all arable farms (cereal monocultures) or on farms that had been entirely entered in the ESA scheme (permanent grassland monocultures).

Generally, introduction of rotational set-aside caused an increase in habitat diversity on the study farms, by introducing another habitat type. Despite this, the overall rotation plan of farms was not greatly affected. However, in one case, a farm cereal rotation was increased from a four year cycle to a seven year cycle to incorporate the set-aside. However, there was no general increase in habitat diversity over the study area as a whole during the study period. It appears that any increase resulting from the introduction of set-aside was counteracted by a decrease in habitat diversity resulting from the uptake of ESA agreements, because several habitat types were often replaced by a grassland monoculture. However, one farmer reported that his uptake of the ESA scheme had, in fact, increased habitat diversity on the farm. Cattle that were grazed on the ESA grassland in the spring and summer required winter feed when they were not at grass in the winter. As a result, kale and fodder beet had been introduced into the arable rotation.

Chapter 4 The Brown hare

4.1 Introduction

In Chapter 2 the brown hare was identified as a potential indicator for monitoring environmental changes in the South Downs ecosystem. This chapter is devoted to a discussion of the brown hare and is divided into five main sections. Section 4.2 reviews literature on the biology of brown hares and related species. It attempts to answer two questions. First, do we know enough about brown hare biology and ecology to use the species as an indicator? Secondly, if it can be used as an indicator, which other species is the brown hare likely to represent? Section 4.3 reviews the methods that have been used to study brown hares. Section 4.4 describes the methods used in the current research to monitor changes in hare populations with the introduction of ESA grassland and rotational set-aside. The results obtained from this investigation are presented in Section 4.5, and discussed in relation to the findings on farm management presented in Chapter 3.

4.2 Brown hare biology and indicator value

4.2.1 Biology

Description of the species

The brown hare (*Lepus europaeus* Pallas) is a small mammal that probably originated in the steppe lands to the north-east of the Mediterranean Sea and then spread across the western Palaearctic region (Corbet, 1986). This increase in its range may have been facilitated by the advance of agriculture. Since neolithic times, farmers have been replacing natural deciduous woodlands with arable and grazing land (Clutton-Brock, 1989), thus increasing the area of steppe-like habitats favoured by the brown hare. It is possible that the brown hare was introduced to Britain, as a game species, by the Romans. There is no evidence that it was present as an indigenous species prior to this time (Corbet, 1986).

The range of the brown hare in Europe is enclosed by the ranges of a number of other *Lepus* species, some of which are so closely related that they may even be conspecific (Corbet, 1986). In Britain, the range of the brown hare can overlap with the ranges of two other Lagomorph species, the rabbit (*Oryctolagus cuniculus*) and the mountain hare (*Lepus timidus*). Where this occurs, the brown hare can be distinguished from both the other species by its behaviour, colour, and longer ears and hind legs. Further details of the descriptions of the European Lagomorphs are given in Corbet and Harris (1991), and below. The brown hare has been successfully introduced into a number of regions, including Australasia (Flux, 1967).

Adult brown hares weigh about three kilograms and an average adult specimen will measure about 60cm from nose to tail (Corbet & Harris, 1991). They moult twice a year; in the summer they have a brown yellow coat, in the winter, a reddish coat (Hewson, 1963). Males (jacks) are generally slightly smaller than females (does), but the sexes are difficult to tell apart in the field. The ratio of males to females in populations is approximately 1:1 (Flux, 1967). Although there is a record of a wild brown hare living for twelve years in Poland (Pielowski, 1971), the average age of European and British hare populations is under one year old and few survive for more than five years (Andrzejewski and Pucek, 1965; Lloyd, 1968; Broekhuizen, 1979). Leverets (young hares) can be distinguished from adults by their size for the first five months, after which time it becomes more difficult. Two methods for identifying the age of dead hares have been used by Frylestam (1980a).

Habitat

In Britain, the brown hare occupies a range of habitat types including agricultural land, rough pasture and moorland (Arnold, 1978). However, arable land supports the largest populations (Tapper and Parsons, 1984). Brown hares may use deciduous woodland and hedgerows for shelter (Bresinski and Chlewski, 1976; Tapper and Barnes, 1986), especially in cold weather (own observations). Brown hares also use coniferous woodland during the winter in Germany (own observation) and probably elsewhere.

Territorial behaviour

The life style of the brown hare has been observed and described in detail by Flux, 1981. Generally, the brown hare is nocturnal. During the day it is solitary and hides in hollows (forms) which it scrapes in arable fields or presses down in vegetation. These forms are often situated on high ground where they provide shelter from the wind while allowing good visibility (Tapper and Barnes, 1986). Often forms are situated away from night-time feeding areas (Tapper and Barnes, 1986). Hares do not dig burrows but rely on keen senses and speed to escape predators. Ownership of a form can change, but hares generally defend the area one to two metres around the form they are currently occupying (Flux, 1981). Other than this, the brown hare is usually non-territorial. Each animal has a home range, the size of which may change throughout the seasons of the year. Estimates of home range size vary between 15 and 50 ha (Flux, 1981; Broekhuizen and Maaskamp, 1982, Tapper and Barnes, 1986). The home range of one animal will overlap with the ranges of others and they congregate to feed in groups at night (Flux, 1981; Schneider, 1981). Group feeding improves the chances of observing the advance of predators (Broekhuizen and Maaskamp, 1982; Monaghan and Metcalfe, 1985) and the mating of females as they come into oestrus (Holley, 1986). There is evidence that a male dominance hierarchy is established within feeding groups (Lindorf, 1978; Monaghan and Metcalfe, 1985). Dominant males guard females in oestrus (Holley, 1986) and, in harsh weather, defend feeding areas against subordinate hares (Lindorf, 1978).

Reproductive biology

Brown hares are able to breed throughout most of the year (Flux, 1967; Lincoln, 1974; Broekhuizen and Maaskamp, 1981). Onset and length of breeding season are controlled by daylength and temperature (Flux, 1967; Hewson and Taylor, 1975; Martinet, 1976; Frylestam, 1980a). The end of the breeding season is probably under the control of daylength, as in the snowshoe hare *Lepus americanus* (Lyman, 1943, as cited in Martinet, 1976). There is a spring peak of sexual activity (Raczynski, 1964; Lincoln, 1974) and during this period brown hares show 'mad March' activity. Males and females congregate in the day-time, and the males initiate rutting activity by jumping and chasing the females. Females that are not quite in oestrus reject the males by boxing. However, these activities probably stimulate the females to come into breeding condition (Lincoln, 1974), and once the females have become sexually active, further rutting activity declines. The percentage of pregnant females is at its highest in the summer and lowest in the autumn (Raczynski, 1964; Lincoln, 1974).

Mating is promiscuous and ovulation is synchronised with mating. Non-pregnant females will be prepared to mate every seven days. The gestation period is approximately 42 days. At birth the doe deposits the leverets in a form. They are precocious, fully furred and their eyes are open. After three to four days they disperse to separate areas of cover and recongregate once a day, half an hour after sunset, to be suckled by the doe (Broekhuizen and Maaskamp, 1976, 1980, 1981). Other than this there is no parental care of leverets. Weaned at four weeks after birth, leverets reach adult size in about five months. These leverets can breed in the year of birth (Raczynski, 1964; Broekhuizen and Maaskamp, 1980), however, most evidence suggests that they usually begin to breed in the year following birth.

Productivity

On average, the brown hare produces three or four litters a year, each containing between two and four leverets. Geographic location, weather conditions, food availability and disease affect the length of the breeding season, and the number of litters that can be produced. These factors also affect the reproductive physiology of the hares, especially the females, and the size of each litter they produce. Litter size will initially depend on ovulation rate and successful fertilisation of ova, but embryonic mortality appears to be influential in the control of leveret production (Pielowski, 1976b). In unfavourable conditions, embryos may be resorbed within pregnant females (Flux, 1967; Pielowski, 1976b). The number of embryos that have been lost can be estimated by comparing the number of corpora lutea with the number of normal embryos developing in a pregnant female (Raczynski, 1964). As embryonic mortality is greater in unfavourable conditions, leveret production is dependent on the time of year that litters are produced; the largest litters occur in early summer, when the weather is generally most favourable (Raczynski, 1964; Flux, 1967; Hewson and Taylor, 1975; Broekhuizen and Maaskamp, 1981). The age of female hares is also influential, with females in their first breeding season showing the widest variation in litter size, and on average, producing the smallest litters. Three-year-old females are the most productive age group (Flux, 1967; Frylestam, 1980a; Broekhuizen and Maaskamp, 1981; Pepin, 1989).

Embryonic mortality as high as 50-80% has been recorded in Poland (Andrzejewski and Pucek, 1965). However, Broekhuizen and Maaskamp (1981) estimated embryonic mortality to be between 6 and 19% in the Netherlands. This is far lower than the Polish value and Broekhuizen and Maaskamp (1981) suggest that length of breeding season is more important than embryonic mortality in the control of leveret production, at least in their study population. There are reports that superfoetation (the presence of different aged foetuses developing in a single uterus) occurs in the brown hare (Raczynski, 1964), but that it is probably insignificant in its effect on the annual production of leverets (Broekhuizen and Maaskamp, 1981).

Post-natal losses of leverets and adult mortality

Abildgard *et al.* (1972, in Denmark) support Broekhuizen and Maaskamp (1981) in their opinion that pre-natal mortality is not an important factor in the regulation of brown hare population size. These views are shared by most other authors, who consider post-natal losses to be of far greater importance (Pielowski and Raczynski, 1976, in Poland; Pepin, 1987, in France; Keith, 1981, in Britain). However, Pielowski (1976b, Poland) observed that the annual mortality of leverets was related to the annual natality (number of births). Thus he argued that pre-natal mortality must play an influential part in control of brown hare population size.

Mortality rate (post-natum) is notably higher in leverets than in adults, but annual fluctuations in the mortality of young brown hares have been observed to follow the same trend as those of the mature animals (Pielowski 1976b). Frylestam (1980a), working in Sweden, found that a brown hare population on an island had a yearly leveret mortality level which was approximately 30% lower than that of a similar population on the mainland. The differences in mortality level may have been due to an absence of predators and traffic, and a reduction in juvenile dispersion with its associated risks (Frylestam, 1980a). The large difference in mortality levels suggests these factors are highly influential in the control of brown hare population size. In four French populations leveret mortality was estimated to vary between 50 and 75% in the period between the birth of the leverets in the spring or summer and their first winter (Pepin, 1989). This author suggests the differences in mortality rates may have been due to different weather conditions and agricultural practices between the four study areas. In the autumn, European populations of brown hares may be composed of between 30 and 60% leverets (Andrzejewski and Pucek, 1965; Pielowski, 1976b; Pielowski, 1981; Lloyd, 1968). The leverets produced in the summer have the best chance of surviving (Kutzer and Frey, 1981)

Adult mortality was estimated at 19.4% over the breeding season and 5.4% over the winter in a Polish study area (Pielowski, 1981). These values for adult mortality are low, however, compared with estimates of 38 to 58% from other European study areas (reviewed by Broekhuizen, 1979). The wide variation is not satisfactorily explained.

Factors affecting hare productivity, and adult and leveret mortality

Productivity and mortality are population processes. They determine the size of hare populations and in turn are controlled by a number of factors. Keith (1981) reviewed population data on a number of Holarctic hare species, including the brown hare, and concluded that food availability and predation were the factors most influential in hare ecology. In some populations and species the effect of these factors may be density dependent. These and other influential factors are discussed below.

Food

Hares are exclusively herbivorous. They can utilise even low grade vegetation by caecotrophy and hind gut fermentation. This process is described by Pehrson (1983) for the mountain hare (*Lepus timidus*), but the biology is identical to that of the brown hare. Brown hares flourish when there is a diverse and plentiful supply of wild plants, grass and early growth-stage arable crop vegetation available throughout the year (Frylestam, 1986; Tapper and Barnes, 1986). Wild plants, when available, are preferred to cultivated crops (Frylestam, 1986). Hares move around farms during the year exploiting the most palatable vegetation available, as their preference for cereals tends to decline once the plants have developed beyond the tillering stage

(Tapper and Barnes, 1986). For these reasons, monoculture arable systems tend to produce an abundance of food for a few months after cereals are sown in the autumn or spring, but can result a shortage of digestible food later in the year. Areas of low crop diversity or monoculture farmland support less dense hare populations (Tapper and Barnes, 1986) and as individual hares in these areas are likely to have lower body weights, their reproductive physiology will be adversely affected (Frylestam, 1980b). Pasture can provide a useful source of food throughout the year (Tapper and Barnes, 1986), although hares move away from grassland soon after it is stocked with sheep and cattle (Frylestam, 1976b; Barnes *et al.*, 1983). There is no clear evidence, however, that hares are in competition with rabbits for food (Broekhuizen, 1975) or are seriously affected by any other aspect of rabbit ecology (Barnes and Tapper, 1986). In some areas, the trend towards monoculture agriculture has caused a reduction in the area of ley grass and an increase in the use of break crops such as oilseed rape (Potts and Vickerman, 1974). Hares tend to avoid oilseed rape in the autumn when it contains antinutritional factors such as glucosinolates (Tapper, 1989), but in monoculture systems may have to feed on it where no other vegetation is available (Frylestam, 1986). In some cases hares can compete with livestock for grazing, damage crops and strip bark from saplings.

Predators

Adult hares and leverets are a major component of the diets of farmland predators, especially the fox (*Vulpes vulpes*), for which species they may make up nearly 50% of the diet (Pielowski, 1976d). Estimates show that foxes can account for the loss of up to 15% of the leverets produced in a year (Pielowski, 1976d, 1981, in Poland; Goszcynski *et al.*, 1976, in Poland; Reynolds & Tapper, 1989, in England) and between 2-4% of adults (Pielowski, 1976d, 1981, in Poland). Domestic pets may also be hare predators, especially on the fringe between towns and farmland (Goszczynski *et al., 1976*). Human predation of hares comes in the form of shooting and hunting with hounds or coursing with greyhounds and lurchers. In Britain, hares are not highly regarded as a game species for shooting, but are sometimes controlled as vermin when populations become very dense. For this reason, there is no closed season for hare shooting in Britain. In some countries of continental Europe, brown hares are shot as an important game and meat resource (Pielowski and Pucek, 1976). In Britain, those who hunt legally with hounds and dogs observe a closed season in the spring and summer when hares are not hunted, but illegal activities by poachers may occur at any time of year. The effect of shooting depends on management. However, hare populations have sufficient reproductive capacity to remain stable despite high shooting pressure (Pielowski, 1976c, in Poland; Pepin, 1987, in France) in one case showing no decline even when 40% of a population was killed each year (Pielowski, 1976c, in Poland). Shooting may result in the death of individuals that would in any case have succumbed to other density dependent mortality factors, such as disease, in unexploited populations (Pielowski, 1976c).

Climate

Weather conditions appear to have little direct effect on hares. They may account for less than 2% of annual leveret mortality and have little or no direct effect on adults (Bresinski, 1976a; Pielowski, 1981). Even in harsh weather conditions, direct starvation of snowshoe hares (*Lepus americanus)* appears to be rare (Smith *et al.*, 1988). However, there may be indirect effects of harsh weather conditions in reducing reproductive capacity (Frylestam, 1980a) increasing the mortality of adults and leverets, since productivity and leveret survival are greatest in the summer when weather conditions are usually at their best. Extreme winter food shortage in American snowshoe hare populations may be an indirect rather than direct cause of death by increasing the number of weak hares taken by predators (Smith *et al.*, 1988). Rainfall and temperature may affect the physiology of hares through influences on plant growth and availability of food (Bresinski, 1976a; Andersen, 1952; Watson and Hewsen, 1975; Frylestam, 1980a; Martinet, 1976). In addition, unfavourable weather conditions may lead to an increased disease risk, especially if hares crowd together in times of food shortage (Barnes *et al.*, 1983).

Diseases

In a Polish brown hare population, disease accounted for 26% of annual leveret mortality and 10% of adult mortality (Pielowski, 1981). Some major hare pests and diseases have been investigated by Broekhuizen and Kemmers (1976) and Kadulski and Dobrynczuk (1976), and reviewed by Tapper, in Corbet and Harris (1991). Coccidiosis (*Eimeria* sp) and yersinia (*Yersinia pseudotuberculosis*), in particular, can result in high mortality. Although hares do not appear to suffer from myxomatosis, a viral disease (European hare syndrome) had a dramatic effect on some populations in the late 1980s (Brown, 1991). More recently some populations have been affected by a disease with symptoms similar to an intestinal disorder called grass sickness in horses (Katherine Wentworth, personal communication).

While acute disease may claim the lives of hares, more chronic disorders may effect populations by reducing productivity. This is illustrated by a study in the Netherlands (Broekhuizen & Maaskamp, 1981) where only 8% of diseased hares were observed to be pregnant, while 80% of the healthy females from the same population were observed to be pregnant.

Pesticides

The use of agricultural pesticides may affect brown hares both directly and indirectly. It has been estimated that 56% of adult hares and 20% of new-born hares in a Polish study area were exposed annually to direct contact with pesticides (Chlewski, 1976). Pielowski (1981) estimated that pesticides were responsible for about 15% of leveret mortality and 2% of adult mortality annually in the same study area. The effects of a number of pesticides have been tested on hares. In these studies, both organochlorine pesticides (Dzilinski and Chlewski, 1976; Mankowska, 1976) and the less-persistent, but more toxic, organophosphorous pesticides (Krynski and Chlewski, 1976) appeared to have little direct effect on adult hare mortality or reproductive physiology under laboratory conditions. However, some of the organophosphorous compounds tested did make hares more lethargic after spraying (Krynski and Chlewski, 1976), which could make them less able to escape predators or agricultural machinery.

Despite a large proportion of hares being exposed to direct contact with pesticides in his study area, Chlewski (1976) did not consider pesticides to be a serious threat. In addition, seasonal preference for crops may have meant that hares were not using crops at times of spray application (Chlewski, 1976). There has also been a suggestion that the smell of chemicals may discourage hares from using recently sprayed crops (Szukiel, 1972, cited in Chlewski, 1976). The studies reviewed above only tested a few compounds on brown hares. Other pesticides may have more toxic effects. For example, there is some evidence that paraquat (a non-specific, total action contact herbicide) has direct toxic effects on brown hares (Tapper, 1976).

Herbicides may affect hares indirectly by reducing the availability of weed food plants on agricultural land (Sotherton, 1992). Although the indirect effects of pesticides on some bird species are well documented (Sotherton, 1992) and their effects on other bird species are the subject of much speculation (O'Connor and Shrubb, 1986), this is an area of research that has not been adequately explored for the brown hare and which deserves further attention.

Mechanisation

Healthy adult hares are able to move out of the way of agricultural machinery and are rarely killed as a result (Pielowski, 1981). Young leverets, however, cannot escape. In France, leveret survival is related to crop type, and the type and timing of cultivation (Pepin, 1989). Leverets hiding in green forage crops, especially frequently mown silage grass, are most at risk (Kaluzinski and Pielowski, 1976, in Poland; Broekhuizen, 1976, in the Netherlands; Pielowski, 1981, in Poland). Reports indicate that up to 17% of the leverets produced in a year may be killed by farm machines (Kaluzinski and Pielowski, 1976; Pielowski, 1981, in Poland).

The effects of road traffic on hares should not be overlooked. In an Austrian study area, between 10 and 15% of the leverets produced were killed annually on roads (Kutzer and Frey, 1981).

Current status

The Brown hare is well adapted to modern agricultural landscapes and it seems unlikely that the deciduous forest ecosystems that existed before the development of agriculture would have provided suitable habitats for it. Records of hares shot on the Holkham Estate in Norfolk (Tapper & Parsons, 1984) show that numbers of brown hares increased to a peak in the late 1800s. This peak coincided with the intensification of agriculture that occurred between 1850 and 1870, when many new farming methods were introduced. Expansion of arable farming at this time produced an agricultural landscape even more similar to the hares' native habitats, and advances in agricultural technology meant that a greater variety and abundance of food was available to wildlife. An increase in hare numbers in Denmark between 1902 and 1952 has similarly been attributed to an advance in agricultural technology (Andersen, 1957).

However, despite continuing advances in agricultural productivity the brown hare population in the United Kingdom has shown a significant decline in numbers since the early 1960s (Tapper and Parsons, 1984). Brown hare populations in other western European countries are declining in a similar way: Denmark (Stangaard and Asfeg, 1980); Sweden (Frylestam, 1976a); Netherlands (Leeuwenberg, 1981); Switzerland (Salzmann-Wendeler, 1976). There is also some evidence of a decline in some eastern European countries: Poland (Pielowski, 1976a, 1981) and Bulgaria (Petrov, 1976). These all appear to be long-term population declines and there is no conclusive evidence that brown hares are subject to cyclical population fluctuations in Britain (Middleton, 1934; Tapper and Parsons, 1984; Tapper, 1987).

Although brown hares are shot as pests in some regions and cannot be said to be an endangered species, their decline in numbers is of some concern as it may be indicative of more general adverse effects of human activity, especially technological advances in agriculture. In addition to this, brown hares are an important resource for meat and recreation in many European countries. Significantly decreased populations would have important economic implications (Pielowski and Pucek, 1976; Pielowski and Raczynski, 1976).

Summary of the processes regulating brown hare populations

There is evidence that brown hare productivity may be density dependent above some threshold density (Frylestam, 1980a). However, it seems unlikely that current populations ever reach densities where this could begin to regulate population size. In addition to this, as hares are non-territorial, populations are not regulated by the density dependent processes that control skylark population size (Chapter 5). It seems that in the case of the brown hare, habitat quality plays a very important role in the regulation of populations. Habitat quality will affect the productivity and determine the mortality rate of adult and leveret hares. As discussed above, there is some controversy as to the relative importance of these processes (productivity and mortality) in hare population regulation. Nevertheless, identification of the factors which have had the greatest overall influence on hare population processes over the last thirty years may allow us to establish why hare populations are declining. When these are understood, the process could be stabilised or reversed.

Explaining the decline in brown hare populations

(a) Decline in breeding adults and survival of leverets

As discussed above, leverets in most populations, and adult hares in some populations, are subject to high mortality. Krebs (1986) calculated that a decrease in the annual survival of adult female hares as low as 0.03% would be sufficient to make a stable population begin to decline by as much as 5% a year. He suggested that specific agricultural parameters should be identified and manipulated to see if any decline could be reversed.

So what could be causing increased mortality in hares? Changes in agricultural practice, especially the replacement of rotational farming practices by monoculture systems, discussed in Chapter 1, must be influential as these result in a reduction of the food available for hares. Even if hares are not dying as a direct result of starvation, mortality is likely to be increased in undernourished hares, since they are probably more prone to disease and predation. There is some evidence that recent outbreaks of disease have had a substantial effect on some populations. In addition, both the direct and indirect effects of increased pesticide use and unfavourable weather conditions may be acting with other factors in reducing the hares' ability to survive. The decline in the number of gamekeepers and thus of predator control activities (Potts, 1980) and an increase in farmland predators such as foxes and crows (Game Conservancy Review, 1991; Marchant *et al.*, 1990) must also be having an effect on hare numbers, as hares are a major component of predator diets on farmland. Young leverets, in particular, must be especially vulnerable to predation and death from the increased use of machinery that accompanies modern farming systems.

(b) Decline in productivity

Increased mortality will eventually lead to an overall decline in the leveret production of a population, as the available pool of reproductive females (and males) dwindles. In addition, a population with a younger average age will be less productive that one with more females at the height of their fecundity. However, it is probable that a decrease in the productivity of individual female hares is having a particularly important effect on populations. While changing farming practices, recent adverse weather conditions (Marchant *et al.*, 1990) and other interrelated factors may not kill hares outright, they will affect productivity. The research reviewed above has provided numerous examples showing that, while adult hares can withstand adverse conditions, their reproductive performance is greatly and rapidly affected.

The fact that research to date has failed to identify any one factor that is particularly responsible for declining hare populations, suggests that the decline is likely to be the result of the interaction of many factors.

4.2.2 Indicator value

The introduction to the current chapter raised two questions. First, do we know enough about brown hare biology and ecology to use the species as an indicator? Secondly, if it can be used as an indicator, which other species is the brown hare likely to represent? In answer to the first question, the test of indicator potential value described in Chapter 2 has already addressed many of the criteria for an appropriate indicator species, and shown the brown hare to have considerable potential. In addition, the review of literature on brown hare biology and ecology in the current chapter has shown that there is considerable, if incomplete information on this species, and that a practical test of its indicator potential is worthwhile. This literature review has shown that the brown hare is a common and easily identified farmland species, and that despite its close relationship with agriculture, the species has shown a significant population decline in Britain and continental Europe over the last 30 years. Although a number of factors may be involved, the most influential causes appear to be related to changes in agricultural practices (a number of which have already been discussed in Chapter 3 as occurring in the South Downs agricultural ecosystem).

In answer to the second question, the response of the brown hare to changing farming practices may be representative of the response of other species, in particular other less easily studied herbivorous small mammals such as field voles (*Microtus*) and shrews (*Sorex sp*) which do not thrive in chemically and mechanically intensive farmland (Tapper and Brockless, 1993). As these species provide food for farmland predators such as barn owls, kestrels, and weasels and stoats, the response of the brown hare may act as an indicator of the availability of food and other habitat resources for exploitation by wildlife within the whole downland ecosystem.

As a result it is suggested that monitoring brown hare populations on farmland may:

* indicate differences in the resources available for wildlife between farms with different management systems.

* indicate if any changes in the resources available for wildlife occur as a result of introduced environmentally sensitive farming practices;

* represent the response of other, less easily studied, vertebrate species (such as small mammals) to these effects.

4.3. Brown hare study methods

The practical investigation of the brown hare's indicator potential began with a review of literature for suitable hare survey methods. Much of the published research has been conducted in Eastern Europe, especially Poland, where hares are managed as a game animal and economic resource (Pielowski and Pucek, 1976). In the UK, it is only recently that a declining hare population has inspired survey work.

Survey methods can be classified as (1) absolute quantitative methods, such as test flushing and netting counts, and (2) relative quantitative methods, such as belt assessment, trailing line, night spotlight, and capture, mark and recapture counts.

1. Absolute quantitative methods

(a) Test flushing

In test flushing, hares are driven from large areas (many hectares) by a group of beaters and the number of animals flushed are counted (Szerderjei, 1958, cited in Andrzejewski and

Jezierski, 1966). In practice some animals are not counted because they sit tight and so results of this method should be treated as relative rather than absolute.

(b) Netting (capture and removal)

In this technique, fields are surrounded by nets into which the hares are then driven by beaters. Netted hares are removed and put in transportation boxes by catchers to prevent double counting (Andrzejewski and Jezierski, 1966). These authors, working in Poland, reported that the number of hares passing through the net without being caught was small (about 3%) and that flushing of hares during net-setting was also small, with some of the flushed hares running into the netted area, rather than escaping.

However, exhaustive observations suggest that, as a rule, more of the hares flushed during net-setting escape from the enclosure than enter it (Pielowski, 1969). In addition, a larger proportion (as many as 19%) escape over or through the net than suggested by Andrzejewski and Jezierski (1966). It has been suggested that netting 10% of a study area provides a representative sample (Andrzejewski and Jezierski, 1966).

2. Relative quantitative methods

(a) Belt assessment (zonal taxation)

In the belt assessment survey method, several beaters move in a line across a selected area, of defined breadth and length, causing any hares present to start up from their forms. All the hares flushed from the belt are recorded by one person. The route of the beaters is chosen to run through all habitat types in the study area, regardless of whether they are considered suitable for hares or not. A belt long enough to cover 5-10% of the study area is considered sufficiently representative of the hare population in a given area (Pielowski, 1969).

However, this method has been shown to over estimate hare densities by 20% when compared with a capture and removal study (Pielowski, 1969). Over-estimation occurs because the observer responsible for counting hares can inadvertently include animals beyond the sample area (Rajska, 1968). This becomes a problem especially when the observer is standing at a distance or at an angle from the beaters. The error is likely to be greater when a narrower belt is used or hare densities are low. This method can only be used effectively when crops are short (from the end of harvest to March).

(b) Trailing line (dragline)

This method is similar to belt assessment, but instead of the use of beaters, a 100m line is trailed between two vehicles (Frylestam, 1981) or between two people (Tapper and Barnes, 1986).

(c) Night spotlight counts

In this method, a spotlight is used at night to reveal hares as they feed. The observer is usually stationary and sweeps the light around in a complete circle. Use of a hand-held spotlight from a vehicle to count hares in African savannah (Eltringham and Flux, 1971) indicated that, although this method provided reliable information on population fluctuations, it was not suitable for estimation of absolute densities. However, studies in southern Sweden (Frylestam, 1981) suggest that as hares feed exclusively in open places in spring and autumn, the mean number obtained by night counts is a relatively accurate estimate of population density. The reliability of night counts was tested against the population density estimated by day-time trailing line sampling. The distribution and total numbers of hares recorded did not differ significantly between the two sampling methods except in cases where the light sampled plots were too few and too widely scattered (Frylestam, 1981).

Studies in Switzerland (Salzmann-Wandeler and Salzmann, 1973, cited by Frylestam, 1981) using this method showed that differences in hare numbers between several spotlight counts over a short sampling period (several days) were negligible, but a study period of several weeks or months led to significant differences between counts. Although hares do not migrate (Bieger, 1941; Kokes, 1948; Koenen, 1965, all reported in Andrzejewski and Jezierski, 1966), they move around within their home range as crops reach favourable growth stages, become unpalatable or offer different amounts of cover (Tapper and Barnes, 1986). This, coupled with changes in weather, may account for the differences observed.

Further investigations in Sweden (Frylestam, 1981) show that:

1. Night spotlight counts are only suitable for use in open areas as woods and scrub produced blind areas.

2. Sample plots should be representative of the proportions and types of different crops in the study area. This is very important when counts are used to estimate the absolute population of an area.

3. Sufficient areas should be sampled to detect the hares on different nights as they move or form groups within their home ranges.

4. Replicate counts should be carried out within a short period of time (Frylestam suggests a fortnight) and under similar weather conditions.

More recent studies (Barnes and Tapper, 1985) have further refined the spotlight count method. Hares are counted with the aid of a 100 watt spotlight which is mounted on a four-wheel drive vehicle. Once the vehicle reaches a sampling point and is stationary, the spotlight is swept around in a complete circle. Any hares present in the beam can be detected by their eye-shine and body shape at up to 300m through 7 x 50 binoculars. These authors have used this method for much of their hare research (Barnes *et al.*, 1983; Tapper and Barnes 1986; Reynolds and Tapper 1989). Hares in each field in the study areas were counted, with not less than 30% of the total area being sampled (Stoate and Tapper, 1989).

These studies confirm that the spotlight method can only be used in the winter months (from after harvest until March) when crops are short. Population estimates based on spotlight count data are very dependent on weather conditions, which affect visibility as well as hare activity. Barnes and Tapper (1985) estimated visibility before and after each count by measuring the distance at which a 1cm square of reflective tape could be distinguished. Spotlight counts were impossible on foggy nights.

Temperature was found to have a significant effect on hare activity and this was taken into account by using a correction factor. Construction of a correction factor is a complicated procedure, so extremes of temperature and other weather conditions are best avoided where possible (Dr Stephen Tapper, personal communication).

Barnes and Tapper (1985) found spotlight counts an appropriate means of assessing large differences between hare populations in extensive studies. Repeated counts in the same area could provide a reasonably accurate measure of population changes over time. The data for the distribution of hares were highly aggregated and conformed to a negative binomial distribution (Bliss and Fisher, 1953), which produced high variance and wide 95% confidence intervals for population estimates. Care was needed in analysing these data. A two-stage method of sampling (after Norton-Griffiths, 1973), where the mean of several samples within each square kilometre were taken and these were then averaged for the study area, gave the most reliable estimates. The effect of 'dead' ground, where hares cannot be seen, can be allowed for by making accurate maps of the area visible in each lamp arc (Stoate and Tapper, 1989).

(d) Capture, mark and recapture

In Poland, hares caught by netting were marked with numbered earmarks and released in the same area. The proportion of marked animals in subsequent catches was then used to estimate population density. As hares are not thought to migrate and there were no reasons to expect higher mortality in marked hares, this method appears to be a reliable way of estimating population densities and the yearly mortality of adult hares (Andrzejewski and Jezierski, 1966)

(e) Other methods

Game bag records. The Game Conservancy National Game Census based upon yearly game bag records has been used since 1961 to monitor the abundance of game species such as grouse, woodcock and brown hares (Game Conservancy, 1991). Although the number of individuals of a species shot will depend on such things as weather and number of shooting days as well as species abundance, the game bag records provide a useful measure of the status of game species.

Radio-tracking. In radio-tracking, a radio transmitter is attached to an animal, and a receiver is used to track the signals of the transmitter as the animal moves about its home range. Although radiotracking is not a practical means of estimating population size, it is extremely useful in the investigation of hare distribution and behaviour, especially during the summer when crops are too tall for direct observation. Tapper and Barnes (1986) used this method to investigate the effects of farming practice on brown hares in England.

Continuous observation. Monaghan & Metcalfe (1985) and Holley (1986) have used continuous observation of hares over many hours with binoculars and telescopes to investigate social interactions, feeding behaviour and reproductive activities.

Indirect methods. Other methods that might provide a measure of hare abundance include counts of pellets or forms.

4.4 Methods used in the current research

The abundance estimation methods described above have been compared to find the most reliable and suitable method for use in a nationwide survey of brown hares by the Nature Conservancy Council (NCC) (Dr Jochan Langbien, personal communication). A one-person transect walk method (based on belt assessment) was chosen as the most suitable on technical merit. This was because the NCC survey was conducted by volunteers walking transects across randomly chosen kilometre squares and while man-power availability was not a limiting factor, technical ability was.

For the present survey, which had to be conducted with limited resources, methods which are labour intensive or excessively time consuming were not considered suitable. The proposed study area was relatively large and so methods conducted on foot were also discounted, although later in the research surveys were conducted on foot. Taking these factors into consideration, spotlight sample counts conducted from a four-wheel drive vehicle were considered to be the most suitable for an extensive survey of hare distribution, abundance and feeding preference.

4.4.1 1991/1992 survey

During a pilot-survey, hare population densities were estimated once for all 17 study farms on winter nights between

November and March 1991/92 (inclusively) when crops were short, using spotlight counts made from a four-wheel drive Subaru truck. A 100-watt, 300,000 candle power white beam bulb (C & D King, Dorking) was used for the spotlight and hares, detectable by their body shape and eye-shine, were counted through 7 x 50 binocular field glasses.

The original plan was to drive to five good vantage points in each kilometre OS grid-square and make a sweep with the spotlight where as much ground as possible could be covered by the beam. In practice this was not feasible. Most farmers had requested that the vehicle stay on the farm tracks, especially in wet weather, and this significantly reduced access and visibility. In some grid squares up to 30% (30ha) of the area could be covered with the lamp, but in others only a very small area could be seen from the track, and some of the crop types in the grid square were not represented in the sample. Over flat areas the spotlight could cover up to 6ha from a point, but in rolling downland, especially if there was tall vegetation or poor visibility, the area covered could be reduced down to less than a hectare if the farm track the vehicle was parked on did not provide a good vantage point. To account for this in the estimate of hare density, the visible area was recorded on enlarged 1:25,000 scale maps. On average 21% of the total area of each farm was lamped, although the area covered ranged between 8% and 48% depending on the size of the farm. Numbers of hares and other nocturnal species were recorded on standard sheets together with records of atmospheric conditions. Depending on farm size, counts generally took between three and four hours to complete.

A population density was estimated for each farm by dividing the number of hares seen by the sampled area:

$$\text{Hares/km}^2 = \frac{\text{no. hares seen}}{\text{area of sampling (ha)}} \times 100$$

4.4.2 The best time of night for counting hares

During the early stages of the project in Winter 1991/1992 the best time of night to see hares was investigated. Three counts were made on one farm on consecutive nights. The first count was started half an hour after dark, the second three hours after dark, and the third five hours after dark. As there was no significant difference between the estimated densities, all other counts were usually made between three or four hours after dark. Counts were never made earlier than half an hour after dark as this is the time at which hares leave their forms for nocternal activity (Broekhuizen and Maaskamp, 1980). There is some evidence that hares become less active as the night progresses, so counts should not be made late at night (Chris Stoate, personal communication).

4.4.3 The best weather conditions for counting hares

Visibility was best when the wind was from the west, especially in light rain. Where possible counts were made under these conditions. However, hares were seen feeding in all weather conditions. Even on very wet and windy nights they continued to feed, but used sheltered areas. There were a number of reports from interviewed farmers that on some nights they saw hares and yet on others there were no hares to be seen. This was probably because of the effects of wind conditions and was compensated for by thorough sampling on adjacent fields during the spotlight survey. In addition, there was little really cold or windy weather during the study period that could have resulted in inaccurate estimates.

4.4.4 1992/1993 survey and 1993/1994 survey

To overcome the access problems encountered in the 1991/1992 pilot survey the sampling method was modified in the winters of 1992/1993 and 1993/1994. Instead of using a vehicle, counts were conducted on foot, using a spotlight with a backpack rechargable solid cell battery. This increased access to the survey area. A red filter was used to lamp stubble fields as it allowed hares to be seen more easily in this habitat type. However, hares were less easy to see through a red filter when against a green background, such as grass or cereals. The filter reduced the extent of the beam and area of visibility. This was corrected for on the record maps.

The improved access, resulting from the change to spotlight counts on foot, meant that now at least one sample could be made in each field or crop type on each farm, regardless of whether the habitat type was considered suitable for hares to feed in or not. In the 1992/1993 survey and 1993/1994 survey an average of 26% of the total area of each farm was lamped (ranging between 9.6% on a large farm and 50.3% on a small farm). On average 5% more of each farm was lamped in the 1992/1993 survey and 1993/94 survey than had been possible in the 1991/1992 survey. The hares were not any more disturbed by a lamp operator on foot than they had been by lamping from the vehicle. They looked at the lamp but did not move away. However, efforts were made not to walk near hares and cause them to move into other sampling areas.

In addition to the record of hare numbers made during the winter 1992/1993 survey, a detailed record was also kept of the habitat types in which the hares were feeding.

4.4.5 The best time of year to count hares

In the second winter (1992/1993) of research an investigation was made into the best time of year to count hares to produce reliable population estimates. During this winter period, each farm was counted three times, in October 1992, December 1992/January 1993 and February/March 1993. During October, autumn field cultivations tended to drive the hares away from some farms. However, the October count gave an indication of the summer populations, before winter mortality. As a result of these findings each farm was only counted once, between November 1993 and January 1994 in the third winter (1993/1994) of research.

4.4.6 Hare behaviour

During the spotlight surveys, hares were seen feeding in loose groups in open fields. However, in the day-time, incisor marks on break and game-cover crops, especially kale and turnips, showed that some hares were also feeding out of sight. These animals could not be seen in the spotlight at night, mainly because of shadows cast by the leaves. One gamekeeper suggested that these tall leafy crops were avoided by the animals in wet weather as they soaked the hares (Nigel Jarvis, personal communication). In dry weather, the presence of these crops may have caused under-estimation of population size.

As has already been noted, the hares did not appear concerned by the spotlight or the sound of the vehicle, and continued to feed. Neither did the approach of an observer on foot scare the animals, as long as care was taken not to get too close or make undue noise. Rabbits, however, fled from the spotlight. This was presumably because they associated the light with shooting. While only four study area farmers (five farms) controlled hare numbers, all farmers controlled rabbits. This was mainly done by night-shooting with a vehicle and spotlight (Appendix C1d).

The hares would look up frequently during grazing, even rising on their haunches to look for predators, as noted by Broekhuizen and Maaskamp (1982) and Monaghan and Metcalfe (1985). In the spring mating activity was observed within the groups. This activity was similar to the observations of Holley (1986). Hares were always observed feeding away from the fields where they rested in forms during the day, as noted by Tapper and Barnes (1986).

4.4.7 Statistical analysis

The group feeding behaviour of hares meant that observations of hare numbers were not normally distributed among the spotlight samples (Appendix C2). As non-normal distribution frequencies of data can affect the validity of statistical tests, the nature of the observed distribution was investigated. Initially the observed distribution was compared against an expected Poisson distribution. X^2 analysis revealed that the observed distribution was significantly different from the expected Poisson (X^2 = 17.61, 2df, $p < 0.001$). This indicated that the feeding hares were not distributed at random. Further analysis showed that the data conformed to a negative binomial distribution (Bliss and Fisher, 1953), . A X^2 goodness of fit analysis (Zar, 1984) was used to compare the observed frequency distribution of data collected in winter 1991/1992 and the distribution that would have been expected if data conformed to a negative binomial (Appendix C2). There was no significant difference between the observed and the expected values (X^2 = 3.13, 1df NS). This aggregated and non-territorial distribution of hares is in accordance with the observations of Flux (1981); Schneider (1981); Broekhuizen and Maaskamp (1982); Barnes and Tapper, (1985).

Once the nature of the frequency distribution was understood, data were transformed to produce a distribution that approached normality. A number of transformations have been described for treatment of negative binomial distributions (Anscombe, 1948; Zar, 1984). However, it was suggested that a logarithmic transformation $\log_{10}(x+1)$ would be the most appropriate for this analysis (Dr Nicholas Aebischer, personal communication) to normalise the distribution and equalise the variances.

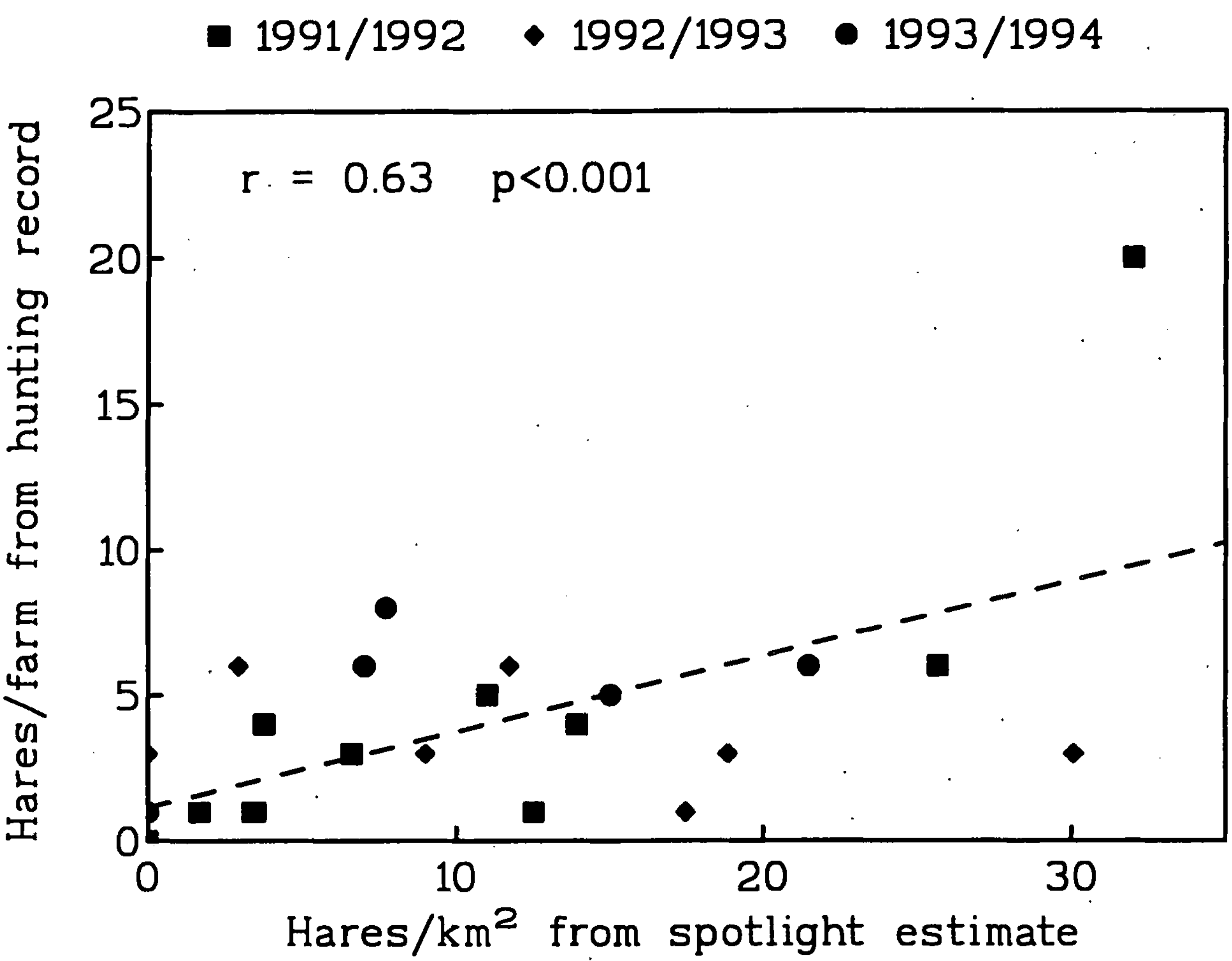
Means are presented ± one standard error, and are arithmetic means. For analysis of hare abundance in relation to habitat diversity (see Section 4.5.2), analyses were carried out by analysis of variance. If interactions were non-significant they were dropped from the model and the analysis was recomputed. SYSTAT 5.0 (Wilkinson, 1990) was used for the analysis, and the acceptance level for statistical significance was $\alpha = 0.05$

4.4.8 The reliability of hare population estimates

A population estimate of hares/km^2 was calculated for each farm in the manner described above. The area sampled on most of the farms was similar, however in a few cases a larger sample area may have resulted in a more reliable estimate of population size as suggested by Zar (1984). This can be compensated for in regression analysis by giving the estimates a weighting which is dependent on sample size. However, it did not appear that sample size significantly affected the accuracy of the estimates and so weighted regression was not considered necessary. Evidence that the spotlight counts were reliable indicators of relative population size on each farm was provided by independent data from three sources.

1. Data supplied by the Brighton and Storrington Foot Beagles (Dr David Brooks, personal communication; Appendix D). The beaglers hunted hares on the majority of the study farms during the winter spotlight count period. They recorded the number of hares seen flushed on each farm by hounds, as part of a national survey for the Masters of Harriers and Beagles Association. There was a good correlation between the two sources of data (Fig 4.1). This graph appears to be highly influenced by the out-lying point. If this point is removed from the regression analysis, the correlation is still highly significant ($r = 0.48$, $p < 0.01$).

Figure 4.1 Correlation between hare densities estimated by spotlight counts on farms and hare numbers from hunting records on the same farms, in winters 1991/1992, 1992/1993 and 1993/1994



2. Shooting record data. Another indication supporting the accuracy of the spotlight counts was provided by data from one of the study farms where hares were shot. An estimate based on a spotlight count made in October 1992 gave 33 hares/km^2, a total population of approximately 154 hares on the farm. In the following winter, the majority of hares on the farm were shot, for reasons discussed later (Section 4.5.2). The total bag exceeded 143 hares (Michael Langmead, personal communication). A spotlight count made in March, after shooting, gave an estimate of approximately nine hares for the same farm.

3. Data from interviews with farmers. Generally farmers and, especially, gamekeepers were accurately aware of the numbers of hares on their farms. They tended to see them feeding at night while rabbit or fox shooting. During the day hares were seen when disturbed from their forms by farm machinery or when flushed during beating on shooting days. There was a good correlation between the numbers reported by farmers and the estimates generated by spotlight counts. In addition, farmers could supply information on hare distribution during the summer, when spotlight counts were not possible because of tall vegetation. From this information. it appeared that populations did not vary greatly during the year on any farm.

4.5 Results

4.5.1 Population trend

Results described in this chapter are based on analysis of data found in Appendix D. Over the three years of study the population trend was one of decline. However, as this was very slight and not significant, the population was viewed as remaining stable over this period. This is illustrated in Fig 4.3.

4.5.2 Factors influencing hare populations

The aggregated distribution of hares among samples was reflected in the distribution of hares among farms. There was a range of population densities among the study farms, with hares completely absent from some farms, especially those close to urban developments (Figs 4.2a-c). The differences in population densities were clearly associated with particular farms. This suggests that particular farm management characteristics were more influential in the ecology of the hares than any geographical or climatic features.

However, there was no single management or biological factor that satisfactorily explained the distribution and abundance of hares. Rather a number of factors appeared to be influential. These were predation and predator control, habitat diversity, food availability and grazing management. These will be discussed in turn, but it should be kept in mind that distribution and abundance patterns of hares were probably the result of a complex interaction of all these factors.

(a) Predators and predator control

Domestic predators. The general absence of hares from farms close to towns (Figs 4.2a-c) was possibly because of poaching

Figure 4.2a Habitat diversity, and hare distribution and abundance in the study area, winter 1991/1992.

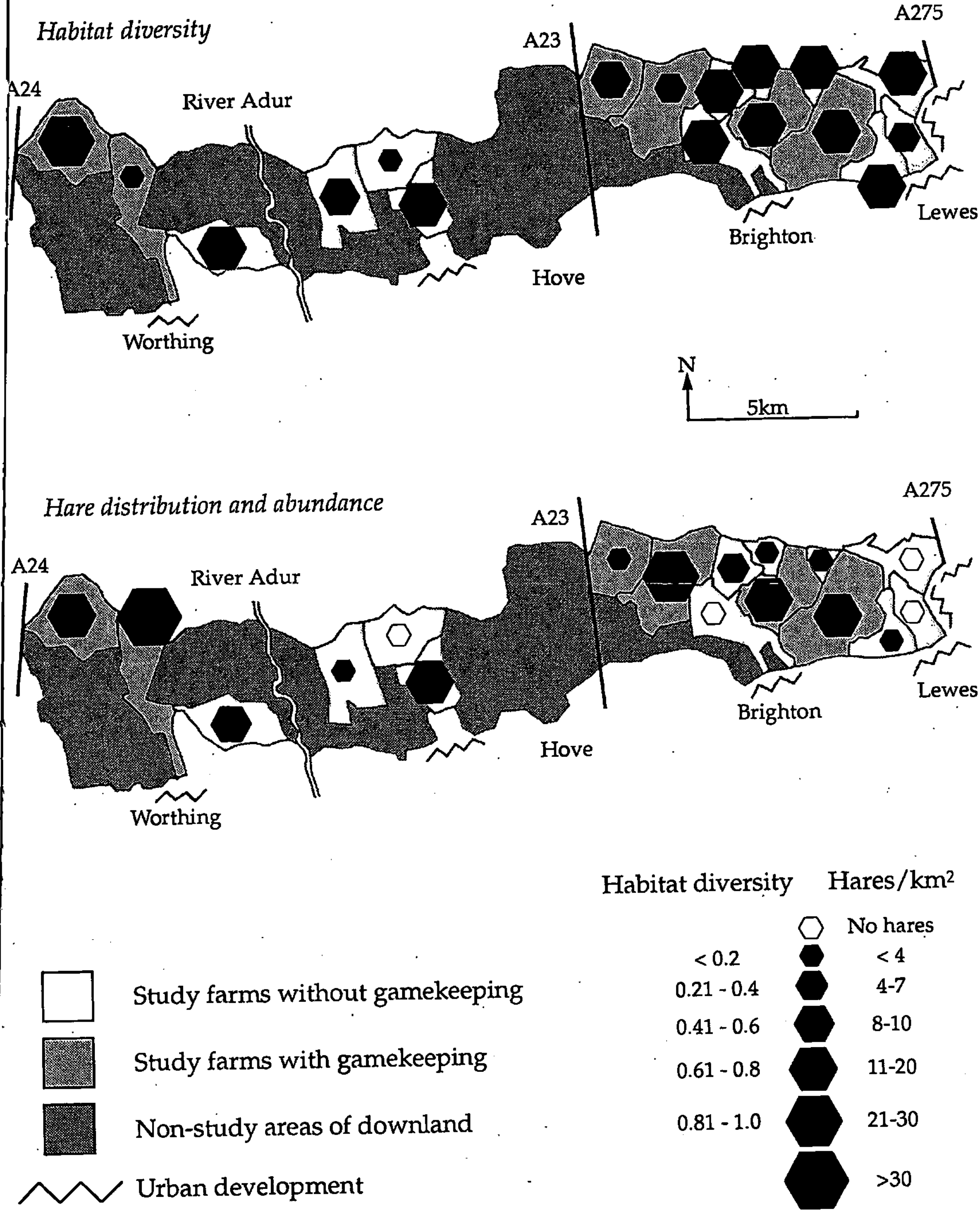


Figure 4.2b Habitat diversity, and hare distribution and abundance in the study area, winter 1992/1993.

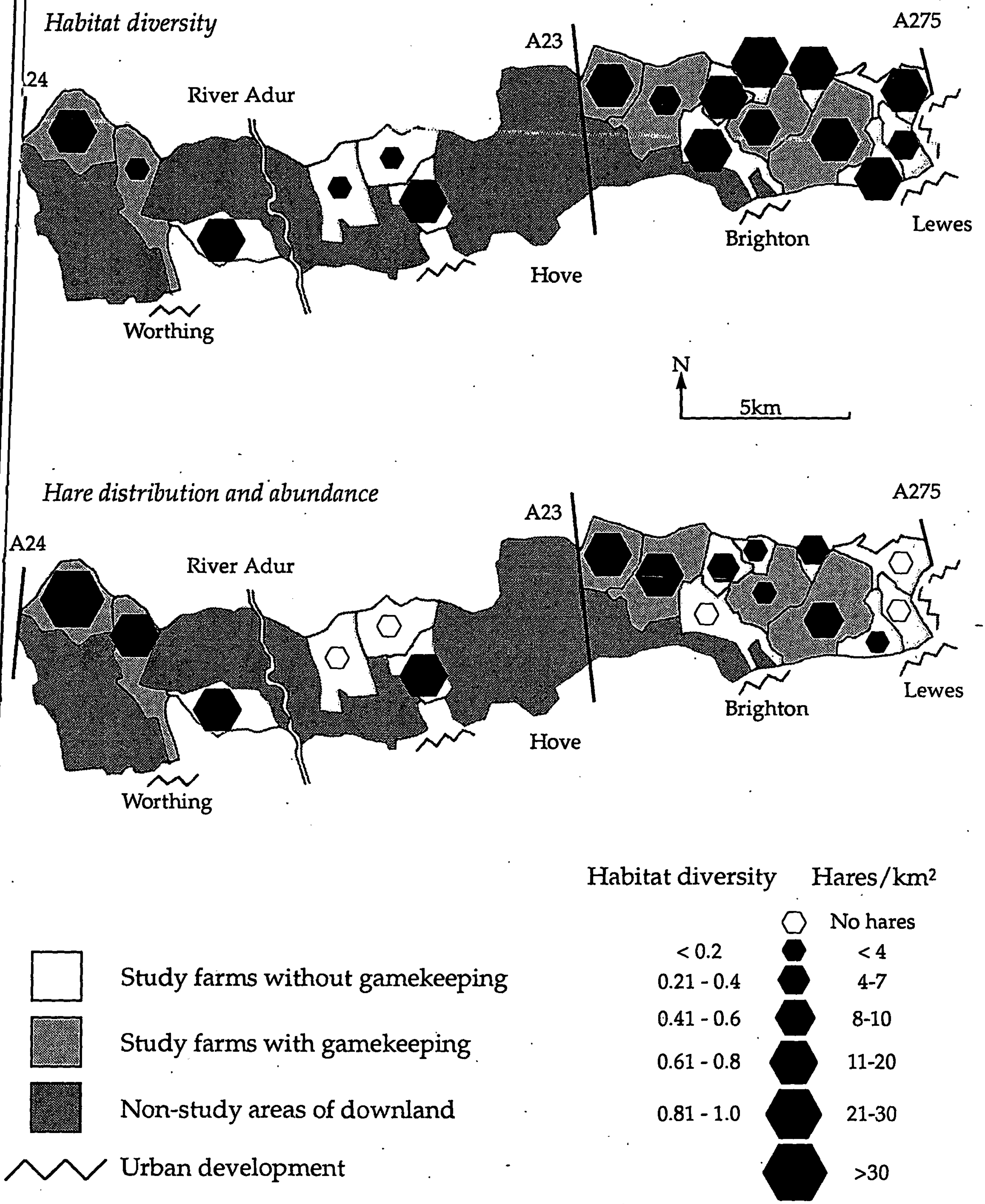
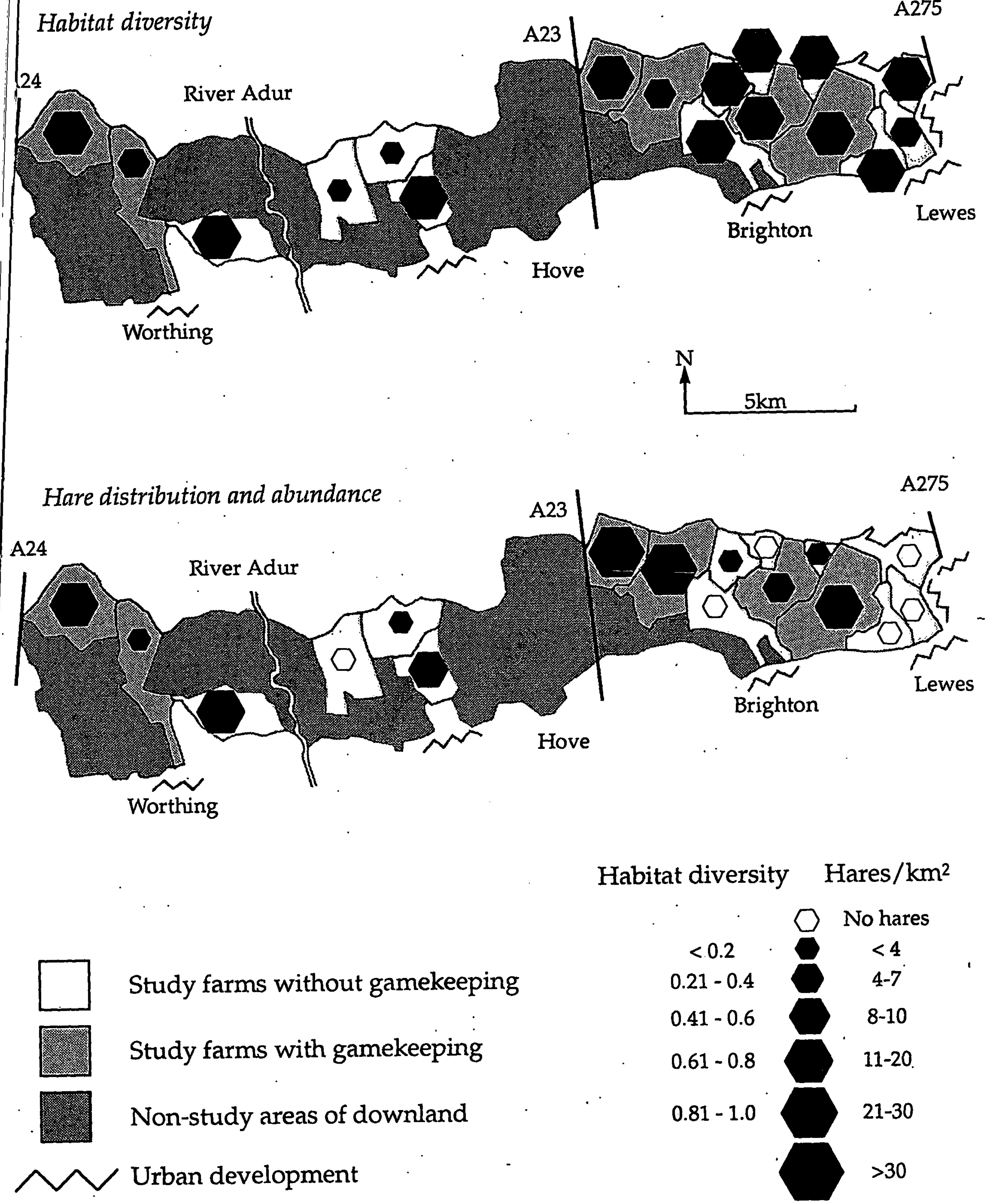


Figure 4.2c Habitat diversity, and hare distribution and abundance in the study area, winter 1993/1994.



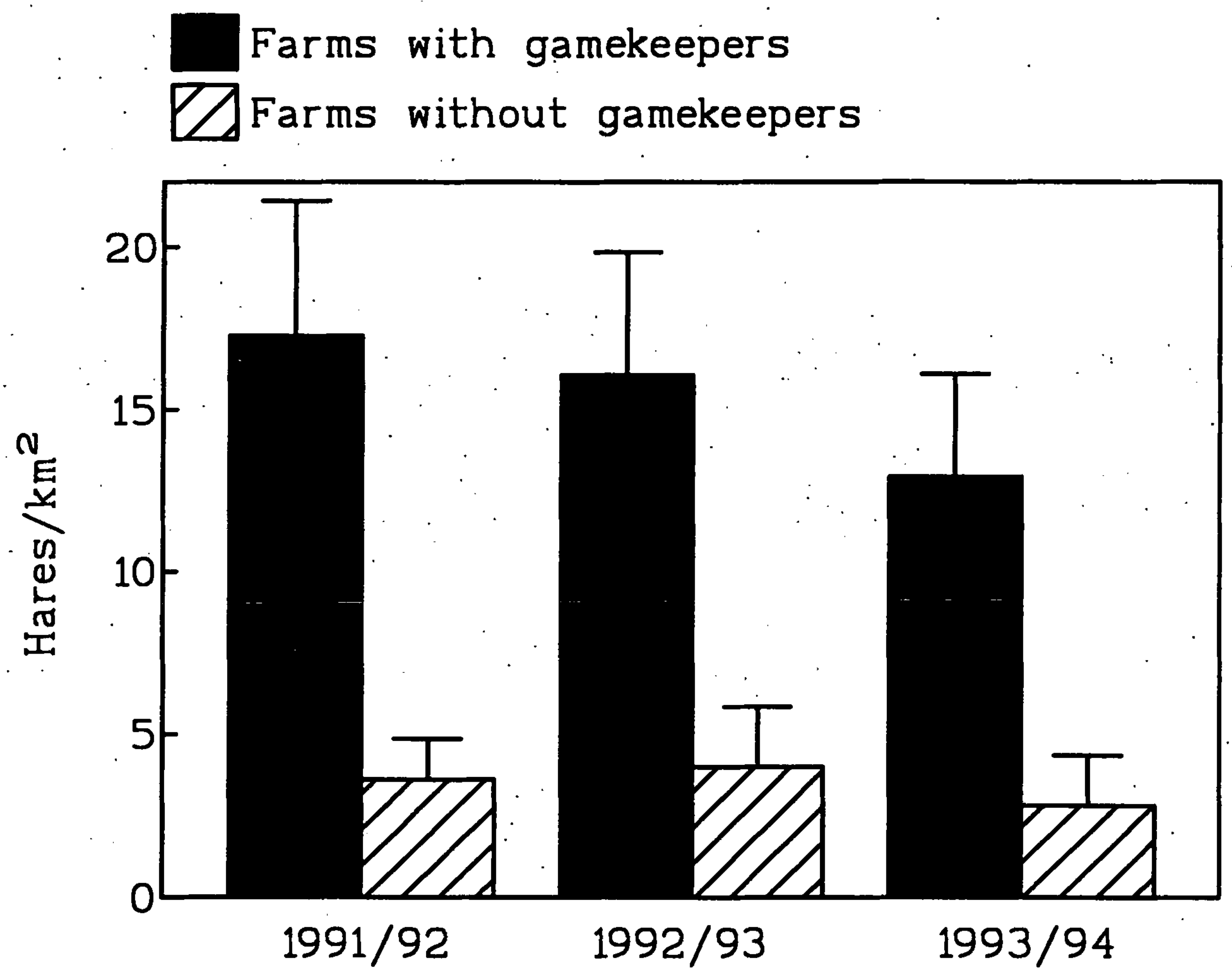
pressure and disturbance by people and domestic pets on the urban fringe. There has been a report confirming that domestic cats are a predator of hares in Poland (Goszcynski *et al.*, 1976). However, there was one notable exception to this trend in the study area, as the farm near Hove showed dense hare populations over all three years of study despite being situated close to the town. This has not been satisfactorily explained.

Gamebird predators. Although none of the study area farmers took any direct measures to encourage hares, the presence of a gamekeeper was a most important factor in the distribution and abundance of hares in the study. Hare populations were dense on farms where the gamekeepers controlled the numbers of gamebird predators such as foxes and reduced the activities of poachers (Fig 4.3). These observations support the well documented effects of fox predation on hare density reported by Goszcynski *et al.* (1976); Pielowski (1976d); Standgaàrd and Asfeg (1980); Reynolds and Tapper (1989); Tapper *et al.* (1991).

Shooting. Over the study period atleast 143 hares were shot on one farm, about 20 hares on each of two other farms and an unspecified number of hares (probably not exceeding five) on another two farms. Hares were shot for a number of reasons: when populations had reached levels that attracted poachers, when required for meat, and occasionally when they consistently spoilt partridge drives by flushing birds in the wrong direction. Although most farmers were satisfied that hares were rarely shot by mistake during rabbit shoots, it was reported to happen occasionally.

Hunting. Poaching, especially coursing at night with lurchers and greyhounds, occurred over much of the study area. It

Figure 4.3 Mean numbers and standard errors of hares/km^2 on farms with gamekeeping and on farms without gamekeeping, in the winters of 1991/1992, 1992/1993 and 1993/1994.



was difficult to quantify the effect of poaching, but on one farm, up to six hares were found that had been killed in one night during spring by coursers (Chris Passmore, personal communication). Coursing can be particularly influential on hare populations, because, unlike beagling, illegal coursing does not have a closed season. In addition some farmers shot hares (see the example discussed above in Section 4.4.6) to reduce the attractiveness of their land to illegal coursers. Farmers were anxious to avoid coursing activity, because of the damage it caused to their farms.

Thirteen of the 17 study farms allowed beagling (legal hare hunting). The huntsman of this pack enjoyed hunting the hares but had no great desire to catch them. As a result his hounds accounted for less than five hares on study farms over the study period and their effect on the population was probably negligible.

Farm livestock predators. All except seven farmers practised some degree of fox control (Appendix C1) to protect livestock, especially sheep. However, on farms without gamekeepers this was either not of sufficient intensity to protect the hares or some other factor had an over-riding effect. In particular, farms close to towns generally had few or no hares even when quite intensive fox control was practised. Conversely, some farms had high hare densities, even when fox control was not practised. In some cases this may have been the influence of hare control activities on neighbouring farms, but this explanation could not always account for the situation.

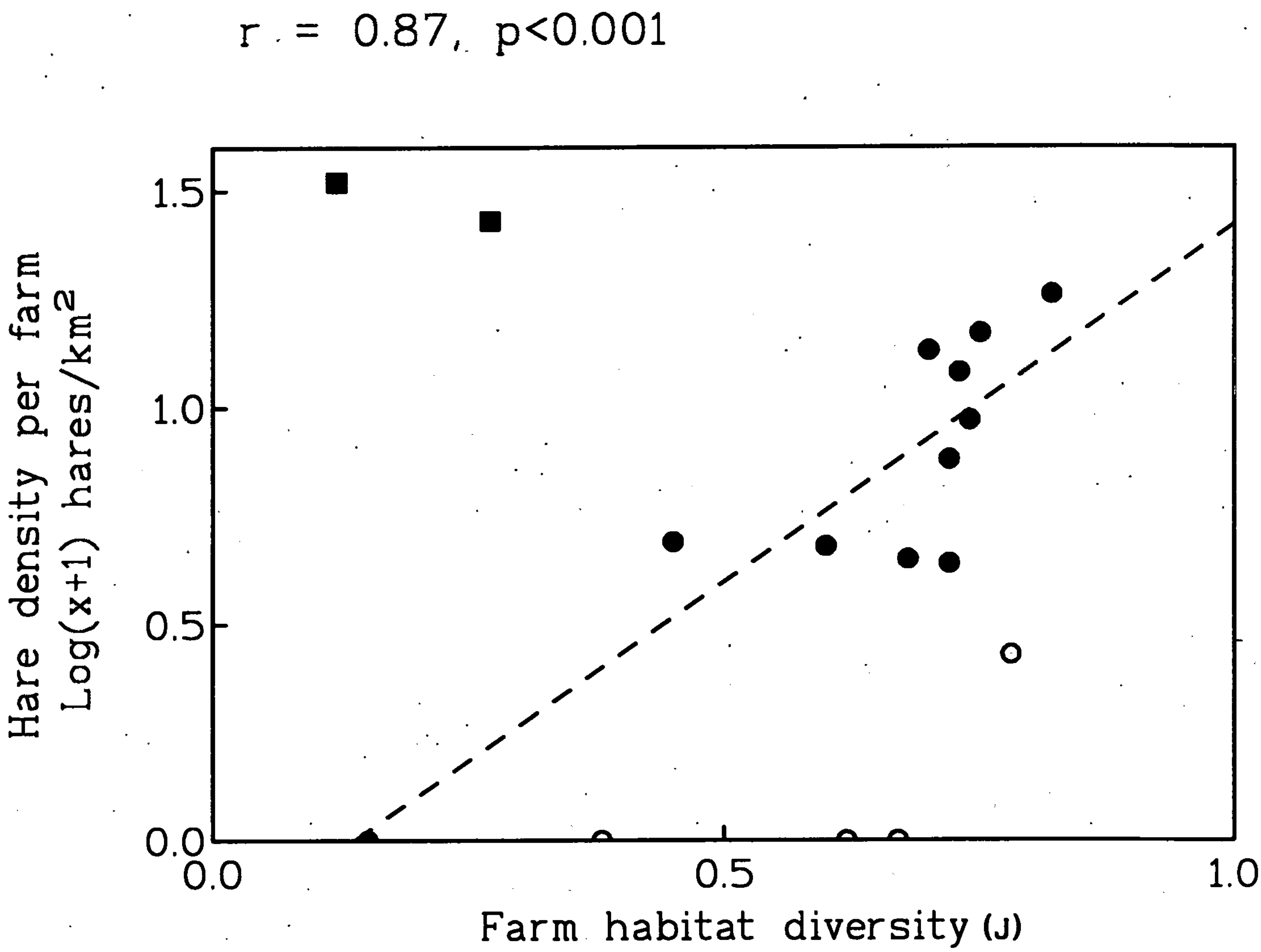
(b) Habitat diversity

So what might have been allowing dense hare populations to survive despite predation? Study of Figs 4.2a-c indicates that generally hare populations are more dense on farms where there is a wider diversity of habitat types. However, more detailed analysis of data from winter 1991/1992 indicated that the distribution and abundance of hares across the study area was not significantly correlated with the diversity of winter habitats on farms. This was a result of two outlying points (solid square symbols in Fig 4.4a) corresponding to two low habitat diversity farms where very intensive predator control allowed dense hare populations to thrive. When these aberrant points were excluded from the analysis, it could be seen that generally there was a significant increase in hare abundance with increasing habitat diversity. In addition, if data from farms close to urban developments (where hare densities were low regardless of habitat diversity, open round symbols in Fig 4.4a) were removed from the analysis, a very significant correlation between hare abundance and habitat diversity was revealed, Fig 4.4a.

A similar, although less significant, correlation between hare density and habitat diversity was apparent in winter 1992/1993 (Fig 4.4b). In winter 1993/1994 (Fig 4.4c) the correlation was not significant.

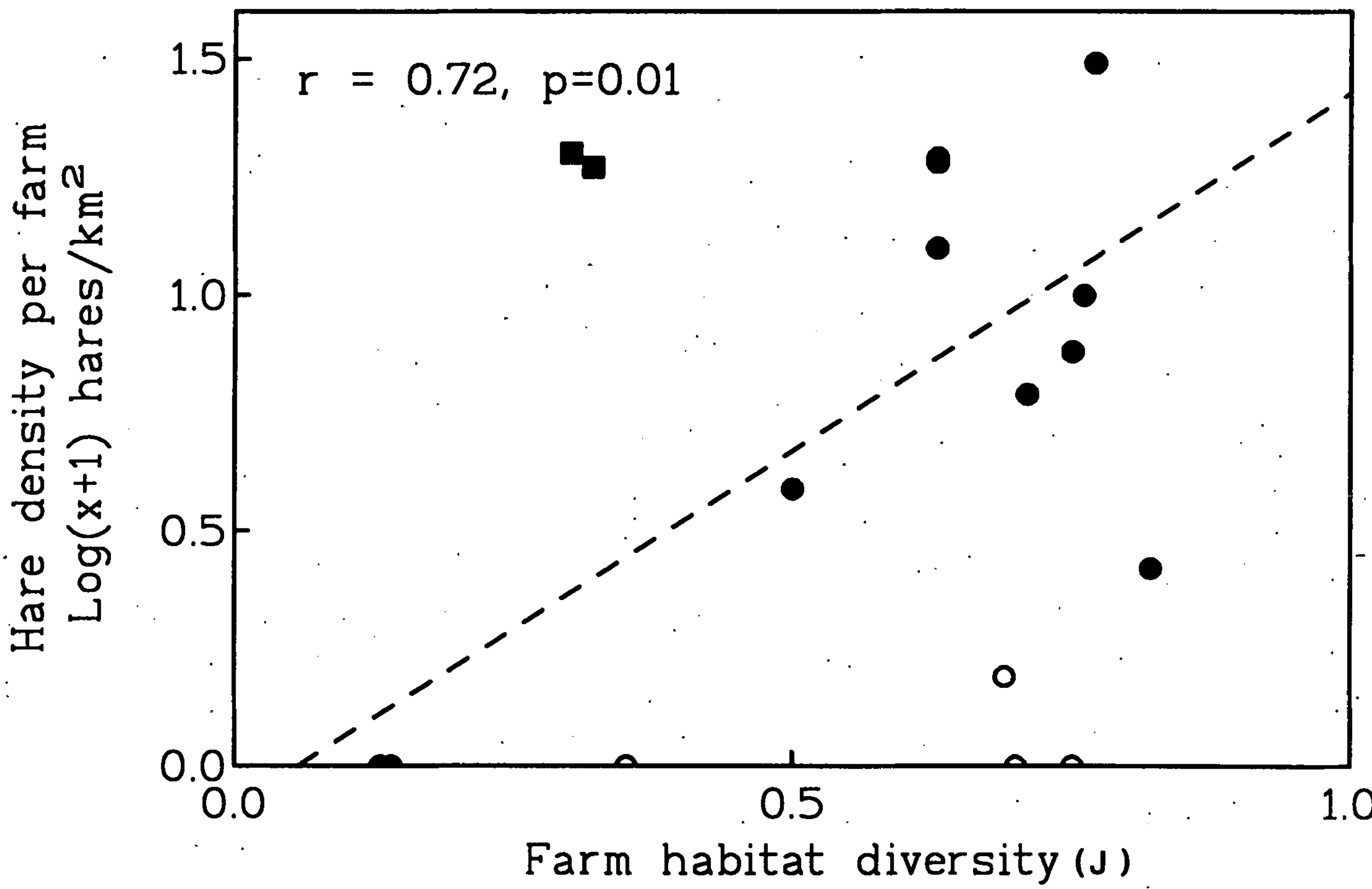
No significant correlation was found between hare abundance and summer habitat diversity, even when the two farms with intensive predator control and the four farms close to urban developments were removed from the analysis. These observations confirm the findings of Tapper and Barnes (1986).

Figure 4.4a Correlation between hare density (hares/km^2) on farms and farm habitat diversity, winter 1991/1992.



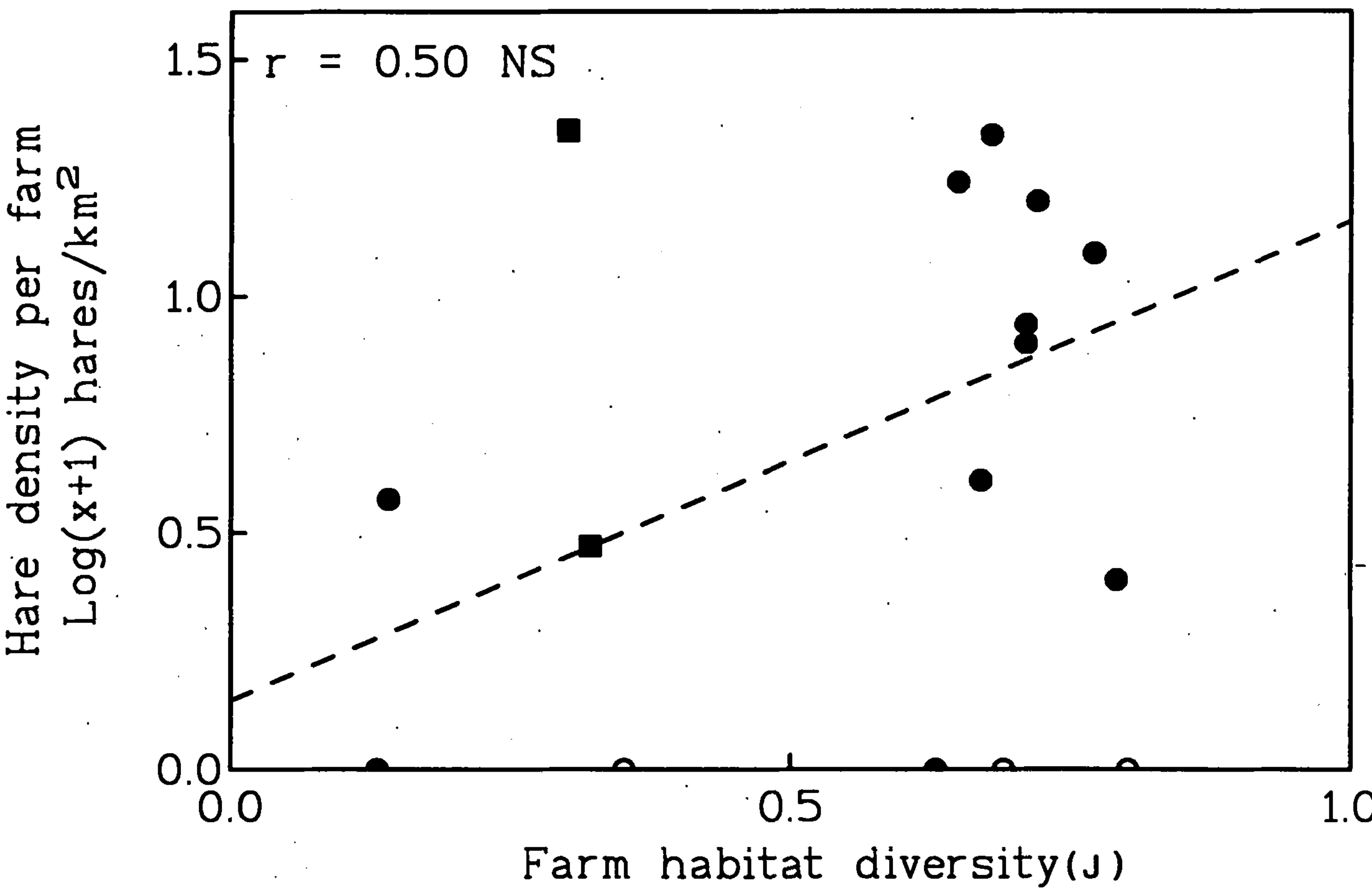
KEY: closed squares = farms with intensive predator control and low habitat diversity; open circles = farms close to towns; filled circles = all other study farms. Habitat diversity is estimated using the Shannon-Weiner measure of relative diversity (J). The correlation analysis is based only on the filled circles.

Figure 4.4b Correlation between hare density (hares/km^2) on farms and farm habitat diversity, winter 1992/1993.



KEY: closed squares = farms with intensive predator control and low habitat diversity; open circles = farms close to towns; filled circles = all other study farms. Habitat diversity is estimated using the Shannon-Weiner measure of relative diversity (J). The correlation analysis is based only on the filled circles.

Figure 4.4c Correlation between hare density (hares/km^2) on farms and farm habitat diversity, winter 1993/1994.



KEY: closed squares = farms with intensive predator control and low habitat diversity; open circles = farms close to towns; filled circles = all other study farms. Habitat diversity is estimated using the Shannon-Weiner measure of relative diversity (J). The correlation analysis is based only on the filled circles.

The habitat diversity indices were constructed using all the habitat types on the premise that wider habitat diversity, regardless of type, benefits hares. Therefore the index included ploughed land even though this habitat type is negligible as a food source. However, it can provide cover, as hares lie in the furrows out of the wind. In addition, its presence on farms where other fields had already been sown indicated that a farm was likely to have a range of arable crops planted at different times. This would then provide a succession of early growth stage cereal crops to satisfy the nutrient requirements of hares (Frylestam, 1986; Tapper and Barnes, 1986).

In support of these findings, analysis of variance revealed that in winter 1991\92 hare abundance was significantly related to the activities of gamekeepers ($F_{2,12}$ = 13.8, p = 0.001), habitat diversity ($F_{1,12}$ = 12.2, p = 0.004) and proximity of urban development ($F_{1,12}$ = 5.0, p = 0.045). In winter 92/93, hare abundance was significantly related to activities of gamekeepers ($F_{2,12}$ = 4.3, p = 0.038) and habitat diversity ($F_{1,12}$ = 5.1 p = 0.044). In winter 1993\94, hare abundance was only significantly related to the activities of gamekeepers ($F_{2,14}$ = 5.8, p = 0.015),

(c) Food availability

During winter 1992/1993 a detailed investigation of hare feeding behaviour was conducted. An indication of the hares' comparative use of particular habitat types throughout the winter, based on the density of hares seen feeding in each habitat type, is shown in Fig 4.5 and, summarised in Table 4.1.

Figure 4.5 Comparative use of a range of farmland habitats by grazing hares in winter 1992/1993, indicated by mean numbers and standard errors of hares/ha of each habitat type. Key: WC, winter sown cereals; DT, downland turf; ST, stubbles; SG, stocked grassland; USG, unstocked grassland.

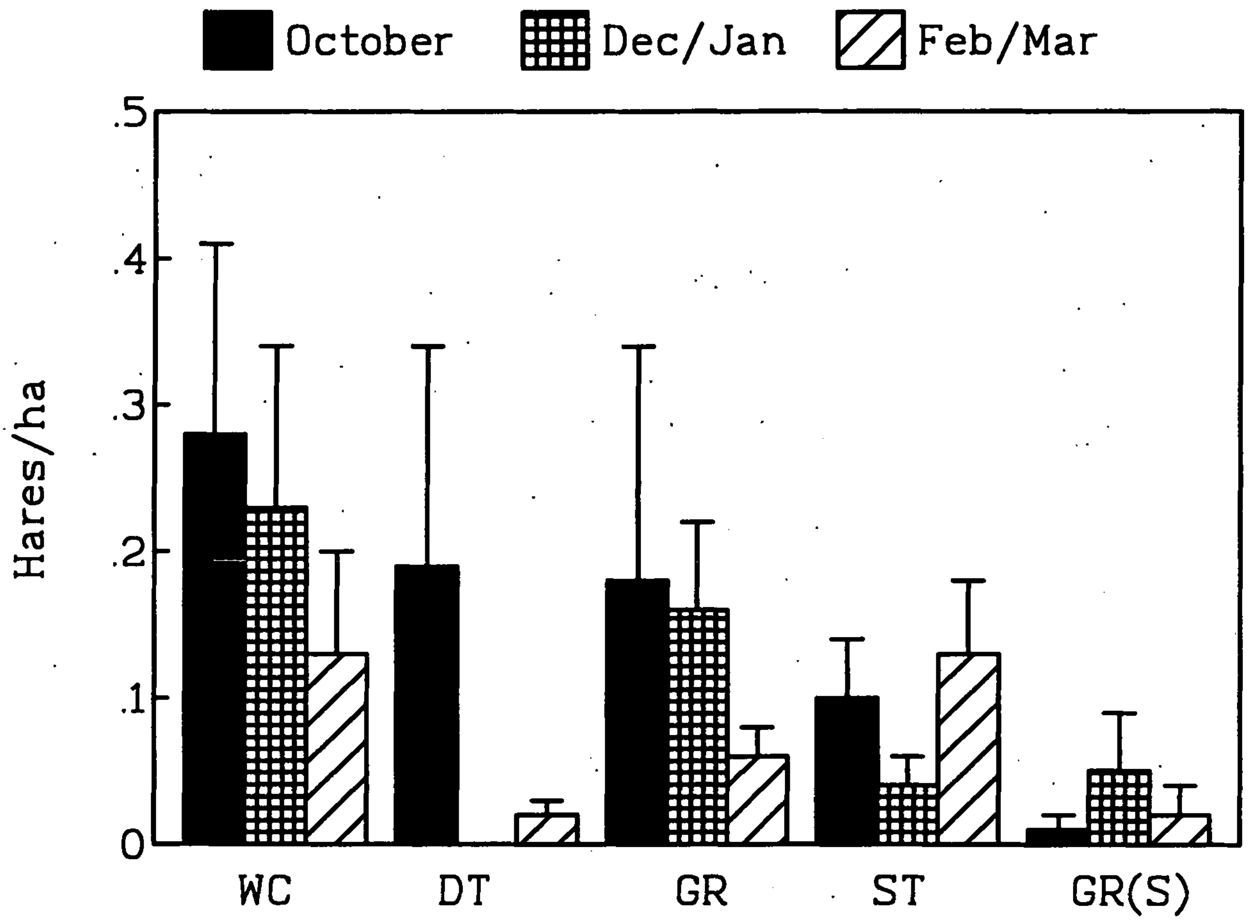


Table 4.1 Summary of the comparative use of farmland habitats for grazing by hares over winter 1992/93. Key: WC, winter sown cereals; DT, downland turf; ST, stubbles; SG, stocked grassland; USG, unstocked grassland. (1 indicates greatest use, 5 indicates least use).

	Comparative use				
	1	**2**	**3**	**4**	**5**
Oct	WC	DT	USG	ST	SG
Dec/Jan	WC	USG	ST	SG	(DT not used)
Feb/Mar	ST	WC	USG	DT	SG

The standard errors shown in this figure are large. Analysis of variance was attempted to further investigate habitat use by the feeding hares, but limited data and a large number of variables meant that there were insufficient degrees of freedom to allow a meaningful interpretation of the results. The information in Fig 4.5 can, therefore, only be used as an indication of the feeding preference of the hares.

Hares moved around farms during the study period, foraging in areas that provided food or the most palatable food. In October, when fields were being cultivated downland turf provided refuge and an important food source, but this habitat type was not used to such a great extent for grazing later in the winter. The hares tended to favour winter cereals and autumn sown grass leys throughout the winter, but especially in December/January when they were at their most palatable. By late February/March, the hares were preferring to feed on stubbles. Perhaps this was because the cereals and new leys had gone beyond their most palatable stage for hares (Tapper and Barnes, 1986) and the stubbles were providing weed species that hares particularly favour (Frylestam, 1986). Before the introduction of set-aside these stubbles would probably not have been available to hares at this time of year. Downland farmers tend to autumn cultivate for both autumn and spring sowing, leaving the fields for spring sowing as fallow plough. In addition, the cessation of straw-burning in 1990 may have provided another source of weed food plants, which would otherwise have been destroyed by the fire.

(d) Grazing management

Although there was no significant correlation between hare density and overall farm stocking density (Table 3.2) in the present study, the way grassland was managed for grazing affected its use by hares. Hares tended to use intensively fertilised non-ESA dairy grassland, especially when it was free of livestock in the winter. However, stocked permanent pasture (whether under or over grazed) and short downland turf were generally avoided, Fig 4.5. The avoidance of stocked grassland has been noted previously by Frylestam (1976b) and Barnes *et al.* (1983). In the present study, feeding hares tended to avoid farms and areas of farms when they were converted from arable crops to ESA grassland. These hares were probably avoiding ESA grassland because, even though stocking density was generally low, these areas were often stocked continuously. Evidence that hares tended to avoid ESA areas during the day-time (ie as areas to situate their forms while resting) was provided by the Brighton and Storrington Beagles. They observed the highest concentrations of hares in the arable areas, not the grassland.

(e) Pesticide use

No significant correlation was found between the intensity of pesticide use on farms and the abundance of hares. This may, however, have been a result of the problems associated with the way in which the intensity of pesticide use was estimated. The intensity of pesticide use was estimated in relation to the way farmers applied pesticides to their winter wheat crop and this may not have been representative of pesticide use on other crop types (see Chapter 3, Section 3.2.2). In addition, other factors, such as predator control, may have over-ridden the effects of pesticide use. However, some evidence that hares favour farms where pesticide use is kept to a minimum was provided by investigations on two of the study farms. The farmers on Farms G and Q had abundant hare populations and used the minimum of farm chemicals. Neither of these farmers practised fox control, but they did use traditional crop rotation systems.

4.5.3 Other factors affecting hare mortality and the production of leverets

Only one farmer questioned could recall ever having found a dead hare. Apparently, this had been killed by straw burning. There were no reports of large scale losses of hares to disease or other factors in this study area.

Many farmers and all gamekeepers reported having seen leverets. Several tractor drivers reported that they took special care to spot leverets and move them from danger while performing field operations, although the leverets often soon moved back to their original location. Several farmers and gamekeepers reported that they had seen very late born leverets over the study period. This may have been a result of very mild winters. One gamekeeper suggested that over the last twenty years there had been a trend towards production of late born leverets. Perhaps hares have adapted to producing young later in the year in response to the introduction of such operations as silage cutting. If this is the case, later born leverets will probably have a lower survival rate as winter food availability is poor and weather conditions less suitable. In addition, the trend towards autumn cultivation and monoculture arable production cannot favour late born leverets. However, introduction of rotational set-aside will provide an additional winter food source in the form of weed rich stubbles.

None of the farmers reported having seen hares or leverets killed as a result of topping set-aside, however several felt that some leverets were probably killed.

4.5.4 Summary of results

The results suggest that the distribution and abundance of hares in the study area was controlled by five main factors (1) predator control, (2) habitat diversity, (3) the availability of food, (4) grazing management and (5) proximity of farms to urban development. The introduction of rotational set-aside was generally beneficial to hares as it provided food and cover in the winter, but topping activities may have resulted in the death of leverets. The introduction of ESA grassland was not beneficial to hares, which moved away from areas as they were converted from arable crops to ESA grassland.

The implications of these findings for the use of the brown hare as an indicator species in monitoring environmental change will be discussed in the final chapter (Chapter 6).

Chapter 5 The skylark

5.1 Introduction

In Chapter 2 skylarks were identified as potential indicators for monitoring habitat quality changes in the South Downs ecosystem. This chapter is devoted to a discussion of the skylark and has five sections. Section 5.2 reviews the literature on the biology of skylarks and related species. As in the case of the previous chapter on the brown hare, it attempts to answer two questions. First, do we know enough about skylark biology and ecology to use the species as an indicator? Secondly, which other species is the skylark likely to represent, and to what extent? The next Section (5.3) reviews methods that have been used to study skylarks. Then Section 5.4 describes the methods which were used in the current research to monitor changes in skylark populations with the introduction of ESA grassland and rotational set-aside. The results obtained are presented in Section 5.5.

5.2 Skylark Biology and indicator value

5.2.1 Biology

Description of the species

The skylark (*Alauda arvensis* L.) is a monogamous ground nesting species (Delius, 1963) Birds of either sex are small and brown in appearance. A detailed description can be found in Coward (1925). Juveniles can be distinguished from adults until their first autumn moult (Delius, 1965), because they have a streaked plumage that makes them inconspicuous when on the ground (Witherby *et al.*, 1938).

Adults are approximately 18 cm in length (Coward, 1925; Witherby *et al.*, 1938) Females are generally smaller than males (Kearton, c1930) and adults can be sexed according to wing length, since males have longer wings than females (Delius, 1965). An average life expectancy of 2.8 years was estimated in a Cumberland study area (Delius, 1965). The average age of the breeding population was estimated as 3.3 years.

Skylarks can be easily distinguished from other Lark species (Alaudidae) that occur in Britain, by their distribution, appearance and behaviour.

Habitat

The skylark is found throughout the Palaearctic region. It is a bird of the open steppes and avoids woodland and scrubland habitats. The species has increased its range across Europe as natural forests have been converted to agricultural land (Hardman, 1974). Although skylarks will use a range of open habitats (Walpole-Bond, 1938) they are most numerous on farmland (Marchant *et al.*, 1990; Williamson, 1967). On Sussex downland farms, skylarks nest on arable and pasture land (Walpole-Bond, 1938). A nationwide survey (Williamson, 1967) found that of these two habitat types arable land was the most preferred. More than twice the density of skylarks was found in association with arable land as with grassland. However, the species is abundant and widespread on grassy areas in the uplands (Williamson, 1967). Use of this habitat type for breeding appears to have increased since the 1940s (Marchant *et al.*, 1990).

Territorial behaviour

Each breeding pair of skylarks nests within a territory, which the male defends with characteristic song-flight behaviour. This song-flight behaviour is discussed in detail in Section 5.4, as it is of central importance to the methods used for surveying skylark populations in the current research.

It has been suggested that it would be difficult to say where any particular skylark was bred as they are a very migratory species (Coward, 1925). However, more detailed studies suggest that skylarks reared in Britain tend to be resident (Walpole-Bond, 1938; Hardman, 1974). Skylarks flock together in winter to feed on stubbles (Walpole-Bond, 1938), but do not leave the country. The skylarks seen moving through the eastern and southern counties of England are thought to be migratory European skylarks (Hardman, 1974).

There is evidence that the resident skylarks tend to return to the same nesting area (often the place of birth) each year. They may even attempt to pair with the same mate as in a previous year and settle in the same nesting territory (Delius, 1964, 1965; Jenny, 1990). In a Cumberland study area pairs remained intact for up to four seasons, although a two season period was the norm (Delius, 1965). There was a strong correlation between the breeding success of a pair in a given season and the likelihood of its remaining a pair in the following season. However, both males and females showed strong nesting site-tenacity and breeding success did not affect their attempts to re-hold the nesting territories of a previous season. In this sand-dune study area, pairs tended to hold the same nesting territory throughout the breeding season.

However, in other study areas there is less evidence of such strong site-tenacity. In some habitat types skylarks can attempt to change territories quite frequently (Schlapfer, 1988; Poulsen and Sotherton, 1993).

Large variations occur in the sizes of skylark nesting territories. Reports indicate that territories ranged between two and five hectares on agricultural land in Switzerland (Schlapfer, 1988; Jenny, 1990). On sand-dunes in Cumberland territories ranged between half and one and a half hectares (Delius, 1965).

In most aspects of their breeding biology skylarks appear fairly consistent in behaviour between populations. So, why are there such large variations in these territory areas ? Similarly, why is site tenacity so great in some habitats and yet in others, the skylarks attempt to change territory quite frequently?

These questions are to some extent answered by reports in the literature. On agricultural land, crop height and density determine where territories are established (Poulsen and Sotherton, 1993), crop type and diversity of crop types determines territory size and site-tenacity (Schlapfer, 1988; Jenny, 1990; Poulsen and Sotherton, 1993). It is worth discussing these factors in more detail, as they appear to hold the key to explaining how skylark population size may be regulated. For this reason, further study of these factors may also allow us to identify the causes behind changes in abundance of nesting skylarks.

Crop type. Territories may enclose one or more crop types (O'Connor and Shrubb, 1986). In Switzerland, there was little evidence that any specific crop type affected where territories were established, but areas near woodland were avoided (Schlapfer, 1988). A predominance of cereals in this study area resulted in this habitat type accounting for 70% of nesting productivity. Other studies, in Britain, suggest that skylarks do prefer some crop types over others, but that preference depends upon what is available (O'Connor and Shrubb, 1986).

In southern England, populations were highest in areas of set-aside (Poulsen and Sotherton, 1993). In addition, productivity (clutch size) was larger in this habitat type. Set-aside was found to support large populations of sawfly larvae (Symphyta, Hymenoptera), which are a major component of skylark chick food. In the same study area, skylark food abundance was lowest in spring barley and adults travelled further for food. This would suggest that territories were larger in this habitat type. However, there is some evidence that skylarks may move out of their nesting territories to collect food (Knight and Shepherd, 1985; Stoate and Szczur, 1993; Chris Stoate, personal communication). The importance of food availability in nesting territory choice has also been observed in Westmorland (Robson and Williamson, 1972). Skylarks chose to nest in grass crops rather than in areas which had recently reverted to arable crops.

The authors suggested that this was because the grass crops had a more abundant invertebrate fauna.

In silage crops, mowing greatly reduces breeding success. This practice destroys nests or reveals them to predators (Schlapfer, 1988; Poulsen and Sotherton ,1993). Intensive livestock production probably has similar effects. Skylark populations decreased in a German study area where pastures were heavily grazed (Busche, 1989).

Crop diversity. In Switzerland territories were smaller in areas where crop diversity was wider (Schlapfer, 1988; Jenny, 1990). In low crop diversity areas, territories were not only larger, but attempts to change territories were more frequent and breeding success reduced (Schlapfer, 1988).

Crop height and density. In Switzerland, skylarks established territories in winter sown cereals until this crop type reached a height of about 25cm in height. They then moved to spring sown cereals, which were at this stage shorter (Schlapfer, 1988; Jenny, 1990). In Switzerland, less dense crops with a ground cover between 20 and 50% were favoured (Jenny, 1990). It appears that dense crops are abandoned because the skylarks cannot walk through them (Schlapfer, 1988). Similar skylark behaviour has been observed in southern England (Poulsen and Sotherton, 1993). The birds deserted winter cereals and grassland when these crops grew too tall or lodged, and moved to spring cereals.

Work in Switzerland suggests that there is little evidence that soil quality or climatic factors affect where territories are established (Schlapfer, 1988).

The research findings reviewed above indicate that territories situated in some habitats result in higher productivity and greater breeding success, that territories in these more suitable habitats are generally smaller, and that mating pairs try to retain them throughout the breeding season.

In summary, these territories tend to be situated in habitats that can provide:

* an open landscape away from trees or scrub
* sufficient plant cover for adults, nests and young birds, but
* vegetation which is not too dense for the adults to walk through,
* a refuge from predators or damage by agricultural machinery,
* a diversity of crop types that can supply sufficient food sources for adults and young.

In less suitable habitats productivity and breeding success are reduced, so regulating population size. In addition, these less suitable habitats result in the need for larger territories to support broods. This also acts as a density regulating mechanism which reduces the number of breeding individuals in a population, as only skylarks with territories breed. This argument is supported by the work of Delius (1965). In the Cumberland study area (Delius, 1963; 1965) birds of both sexes (but especially one-year-old males) that were unable to establish a nesting territory did not migrate to other areas. They stayed as a non-breeding population, which accounted for 10% of the total adult population. These non-breeding adults were not permanently segregated from the breeding population, but remained in reserve. After a hard winter, when some larks had been killed by the cold weather, there were no apparently non-breeding adults. The population was using its full reproductive capacity.

Reproductive Biology

Skylark pairs may produce up to three broods (Walpole-Bond, 1938; Whitherby *et al.*, 1938) between mid-April and mid-July; occasionally later in the year (Walpole-Bond, 1938; Delius, 1965). The males return to the nesting area before the females (Delius, 1965). Elaborate courtship flights, by both sexes, and fighting between males lead to mating (Coward, 1925). The males are rarely damaged in the intraspecific fights (Delius, 1963). The females build the nests by themselves (Walpole-Bond, 1938; Whiterby *et al.*, 1938; Delius, 1963). This is a simple structure of dry grass in a hollow on the ground. The nests are usually situated in crops or tufts of grass. Rarely, a nest may be situated in areas with very little vegetation (Kearton, c1930). The females lay one egg per day, usually in the morning (own observations). Incubation, which is carried out only by the females (Walpole-Bond, 1938; Witherby *et al.*, 1938), begins when the whole clutch has been laid. The females conceal the nest sites by landing some distance from the nest and running through the vegetation.

Onset of laying at the beginning of the season is under the control of daylength and temperature (Delius, 1965). Generally, a first brood is attempted in mid-April (Walpole-Bond, 1938; Delius, 1965). If this is successful a second brood and then a third brood may be attempted. However, because of nest predation up to four or more clutches may be laid to produce even one successful brood (Walpole-Bond, 1938; Delius, 1965).

Average clutch size varies between three and five mottled-brown eggs (Walpole-Bond, 1938; Witherby *et al.*, 1938; Delius, 1965). Second brood clutches are significantly larger than first brood clutches (Delius, 1965; Schlapfer, 1988). Clutches as large as six or seven eggs have been recorded (Delius, 1965)

In a Cumberland study area (Delius, 1965), it was estimated that on average each female annually produced 2.7 clutches of 3.7 eggs. In Switzerland, it was estimated that on average 7.4 eggs were produced in two clutches per year (Schlapfer, 1988). In the Cumberland study area, there was considerable variation in the number of broods undertaken by different pairs in a season (Delius, 1965). Laying of replacement clutches varied between four and six days after nest predation, depending upon the stage at which the previous clutch was lost (Delius, 1965). There was no inhibition of re-laying beyond 17 days after hatching, allowing 'telescoping' of broods. This means that in some cases the males feed fledglings while females incubate another brood. Skylarks have been observed to re-lay in the same nest after predation (Walpole-Bond, 1938). Generally, the female probably builds a new nest. It is not clear what inhibits skylarks from laying at the end of the season (Delius, 1965).

In a successful brood, incubation lasts eleven days (Witherby *et al.*, 1938; Hardman, 1974). The young are non-precocious and remain in the nest for a further nine to ten days after hatching. They are fed by both parents, although, the female does most of this work (Delius, 1963). After leaving the nest, the juveniles cannot fly for at least ten days.

In some cases juveniles have been observed to breed in the year of birth (Delius, 1965), although it is more common for sexual maturity to be reached in the year after birth.

In the Cumberland sand dunes (Delius, 1965) breeding success (this is the percentage of eggs laid which survive to independent juvenile age) was estimated at 46%, and breeding success was twice as great in older females than in one-year-old birds. In Switzerland, breeding success was estimated at 37% in one agricultural study area (Schlapfer, 1988), and at 25% in another (Jenny, 1990).

Adult and juvenile mortality

The most extensive study of skylark mortality was carried out over five breeding seasons in Cumberland (Delius, 1965). Mean annual mortality of both male and female adult skylarks was estimated as 33.5%. There was no significant difference between male and female mortality. Highest mortality occurred in cold winters. When the effects of these cold winters were excluded, average annual adult mortality was estimated at 30%.

Delius (1965) gives a mortality value of 32% for egg losses and a mortality value of 33% for nestling losses. The mortality rate of juveniles between nest-leaving and the end of the first year was similar to that of the adults (about 30%). Mortality rate did not change with age after the end of the first year.

Factors affecting skylark productivity, and adult and juvenile mortality

Food

Skylarks feed by walking along the ground collecting food from the soil surface or pecking at the vegetation (Green, 1980; 1987). During the autumn and winter adult skylarks feed on weed seeds, cereal grains after harvest or at sowing time, seedlings and leaves. In the spring and summer they feed on invertebrates, especially beetles (Coleoptera), grass flowers, leaves and seeds (Coward, 1925; Walpole-Bond, 1938; Witherby *et al.*, 1938; Green, 1980;1987). The chicks are fed on sawfly larvae (Symphyta) for the first five days of life. After this they are fed on beetles (Poulsen and Sotherton, 1993).

Predators

Adult skylarks are not intensively predated on farmland, although skylarks are sometimes taken by merlins (*Falco columbarius*). However, in common with many other species of small bird, they suffer very high clutch and brood mortality (Walpole-Bond, 1938), much of which is due to predators. Predation has been estimated to account for 85% of egg losses and 90% of nestling losses (Delius, 1965). The main predators are Corvids and farmland predatory mammals (Delius, 1965). Predation of skylark nests by Corvids is density dependent, and nests close to woodland are particularly at risk (Moller, 1989).

Climate

The skylark is generally a hardy species. Cold weather and rain do not seem to affect egg or nestling survival. However, the adults are unable to withstand cold winters. Dramatic declines in population size can occur as a result of this (Delius, 1965; Marchant *et al.*, 1990).

Diseases

There is very little reference to skylark diseases or pests in the literature and disease appears to play a generally insignificant role in the ecology of this species (Delius, 1965).

Pesticides

There is much evidence that the direct toxic effects of pesticides have significantly influenced population sizes of some bird species. An example is the peregrine falcon *Falco peregrinus* (Ratcliffe, 1980). The indirect effects of pesticides on some bird species are also well documented. High pesticide input reduces the availability of weed plants and arable invertebrates (Sotherton, 1992) which many bird species rely on for food. This is particularly influential in the breeding success of grey partridges *Perdix perdix* (Aebischer, 1993). The increased productivity of skylarks in habitats with more abundant insect populations indicates that this species is indirectly affected by pesticides in a manner similar to grey partridges.

Current status

Up to 1938, skylarks were extremely abundant in Sussex throughout the year (Walpole-Bond, 1938). This author records that a thousand dozen skylarks were netted on the Downs near Brighton *before noon* on a day in January 1897. These birds were sold as a delicacy to France.

Since 1961 the British Trust for Ornithology (BTO) has used the Common Bird Census (CBC) to monitor the status of British breeding birds, including skylarks. With the exception of low population numbers in the early 1960s, 1979 and 1982 (which were due to cold winters), the national population remained relatively stable until 1980. Since then the population has declined to half that recorded in the 1970s (Marchant *et al.*, 1990, and data used by Poulsen and Sotherton, 1993). Similar recent declines in skylark populations on agricultural land have been reported in Belgium (Paulussen, 1993), Schleswig-Holstein in Germany (Busche, 1989) and Switzerland (Schlapfer, 1988). Similar declines have occurred in a number of other farmland bird species such as the meadow pipit *Anthus pratensis*, lapwing *Vanellus vanellus*, linnet *Carduelis cannabina*, and grey partridge, *Perdix perdix* (Marchant *et al.*, 1990). Corn buntings *Miliaria calandra*, in particular, have declined in a very similar manner to skylarks. It should be noted that there is no evidence of cyclical population fluctuations in any of these species.

In Britain, skylarks are currently the twelfth most numerous breeding bird species and the *most* widely distributed. The national population has been estimated as approximately two million pairs (Marchant *et al.*, 1990).

Earlier this century the species was not generally considered to be a crop pest (Coward, 1925; Walpole-Bond, 1938). However, despite the population decline, skylarks now cause considerable crop damage, especially to sugar beet in East Anglia (Hardman, 1974).

Summary of the processes regulating skylark populations

It appears, therefore, that population size can be regulated by:

* the number of adults in the population; this determines basic reproductive potential,

* the quality of habitats where territories are situated; this determines adult survival, productivity and the breeding success of broods,

* the number of territories available; this affects overall productivity, as only adults with a territory breed.

Explaining the decline in skylark populations

It is likely that the decline in skylark populations is a combination of all three of the population regulating processes summarised above.

In any species, a progressive decline in population size would eventually result in a decrease in available breeding adults. However, it seems unlikely that there has been a reduction in breeding adults which could have *initiated* the skylark decline. By comparison with clutch and brood mortality, adult mortality is relatively insignificant in skylark ecology.

One factor that could possibly have increased adult mortality is cold winter weather. It has been reported that winters have become generally colder and more severe over the last 50 years (Marchant *et al.*, 1990). However, other cold sensitive species such as goldfinches *Carduelis carduelis* have not shown such significant declines (O'Connor & Shrubb, 1986).

Adult populations may have declined as a result of changes in agricultural practices. These have lead to a reduction in food sources for the adult birds of many species. In particular, the use of pesticides (Sotherton, 1992), improved harvesting efficiency, and decline in winter fallows (O'Connor & Shrubb, 1986) appear to have been influential in the population declines of several farmland species. It may be this loss of traditional food sources that has increased the necessity for skylarks to feed on crops and caused them to become a crop pest.

However, the decline in skylark populations is probably more greatly influenced by reduced productivity and breeding success. As has been summarised above, this is dependent upon number of available territories and the quality of these territories. For most bird species, territory availability is reduced by habitat replacement for agricultural purposes or by increased urbanisation. In the case of skylarks it seems unlikely that destruction of habitats, such as hedgerows, will have had much effect. Theoretically, increased areas of arable monoculture should suit this stepe species. However, urbanisation will have had some effect. For example, there are reports of skylark nesting areas being lost to road building (Busche, 1989).

On the other hand, there is strong evidence that as a result of agricultural practices territory quality has been reduced.

This in turn may have reduced productivity and breeding success to the point where populations started to decline. Modern arable production systems appear to reduce territory quality mainly by reducing food sources for nesting birds. First, they reduce the diversity of crop types and the associated food sources. Secondly, these production systems require high pesticide inputs which affect food chains in the agricultural ecosystem and reduce the availability of food species for skylarks and other wildlife.

In addition to reducing food sources, modern agricultural practices have increased the destruction of broods by an increase in agricultural mechanisation. On grassland, the replacement of hay making with silage production means that grass is now cut in the middle of the breeding season, and more frequently. The nests are destroyed directly or revealed to predators, and breeding success is significantly reduced. The cutting of set-aside, which is a condition of the scheme, has a similar effect. Increased intensity in grazing systems also reduces cover for nesting.

Perhaps linked with agricultural change and a decline in gamekeepers (Potts, 1980), has been a dramatic increase in farmland predators (Game Conservancy, 1992; Marchant *et al.*, 1990). As skylark breeding success is so heavily influenced by predation, the increase in predators must be influential in the population decline.

5.2.2 Indicator value

As for Chapter 4, on the brown hare, the introduction to the current chapter raised two questions. First, do we know enough about skylark biology and ecology to use the species as an indicator? Secondly, if it can be used as an indicator, which other species is the skylark likely to represent? In answer to the first question, the test of indicator potential value described in Chapter 2 has already addressed many of the criteria for an appropriate indicator species, and shown the skylark to have considerable potential. In addition, the review of literature on skylark biology and ecology in the current chapter has shown that there is considerable, if incomplete information on this species, and that a practical test of its indicator potential is worthwhile. This literature review has shown that the skylark is a common and easily identified farmland species, and that despite its close relationship with agriculture, the species has shown a significant population decline in Britain and continental Europe over the last 20 years. Although a number of factors may be involved, the most influential causes appear to be related to changes in agricultural practices (a number of which have already been discussed in Chapter 3 as occurring in the South Downs agricultural ecosystem).

In answer to the second question, the response of the skylark to changing farming practices may be representative of the response of other species, in particular ground nesting, insect and seed eating species, such as meadow pipits (*Anthus pratensis*), partridge species (*Perdix perdix* and *Alectoris rufa*) and corn buntings (*Miliaria calandra*). The skylark will probably be less representative of scrub and canopy nesting species such as mistle thrushes (*Turdus viscivorus*), linnets (*Carduelis cannabina*) and warbler species (Silvidae), although, some members of the latter group use agricultural land close to hedgerows and woods to feed. Therefore, areas that provide an abundance of food for skylarks will also provide food for these species. Skylarks will be generally less representative of predatory bird species such as kestrels (*Falco tinnunculus*) and crows (*Corvus corone*). However, a decline in skylarks may indicate a decline in the resources available for wildlife in the downland ecosystem, especially in the food chains. Eventually species in the higher trophic levels will also be affected.

As a result it is suggested that monitoring skylark populations on farmland may:

* indicate differences in the resources available for wildlife between farms with different management systems.

* indicate if any changes in the resources available for wildlife occur as a result of introduced environmentally sensitive farming practices;

* represent the response of other, less easily studied, bird species to these effects.

5.3 Skylark study methods

The literature does not contain description of any methods specifically for estimating skylark abundance and monitoring their nesting behaviour over extensive study areas, although a number of bird census techniques (including point and transect census methods) that could be applied to skylarks have been reviewed by Bibby and Burgess (1992). Most studies have been conducted over relatively small areas and rely on the flushing of birds or continuous observation over periods of time (Delius, 1965; Green, 1980; 1987; Marchant *et al.*, 1990). However, a method for estimating numbers and sizes of territories has been described (Marchant, 1983), and extensively used in the British Trust for Ornithology's (BTO) Common Bird Census (CBC). The locations at which members of a breeding pair are observed are mapped during ten visits to an area. The mapped location points are then enclosed with a line to indicate the boundaries of each territory. The method has been applied to many species, but is particularly reliable when applied to skylarks, which perform readily observed territorial behaviour and nest in the open.

5.4 Methods used in the current research

The method used to estimate skylark abundance in the current research was based on the territory guarding behaviour of male skylarks, and this behaviour is discussed here in detail. Male skylarks defend their nesting territories with a characteristic song-flight. 'The bird rises with quivering wings, beginning the song when a few feet up; then its whole body vibrating with energy, it mounts higher and higher, often drifting round in a wide arc before it descends, still singing. When yet at a height, the song ceases and the bird drops abruptly, recovering itself a foot or so above the grass and skimming forward before alighting' (Coward, 1925).

The 'vehemence and continuity [of the song] are remarkable' (Coward, 1925) and skylarks are able to mimic the song of other birds to some extent (Coward, 1925; Walpole-Bond, 1938). Male skylarks may sing throughout much of the year, but especially during the nesting season. At this time of year song-flights may be made from before dawn until dusk (Coward, 1925) and even at night (Walpole-Bond, 1938). The males may also sing from the ground or suitable perches such as fences or walls. It is rare for them to sing from trees or bushes. Ground song occurs especially when the birds are pairing (Coward, 1925; Clark, 1947). During courtship rival males sing vigorously while fighting (Coward, 1925).

Although there are reports of occasional song behaviour in female skylarks (Delius, 1963), there are no reports that females perform true song-flights. Similarly, there is no evidence that juveniles or adult males without a territory perform true song-flights.

An average song length of 2.2 minutes has been estimated (Rollin, 1931). Length of song increases as the breeding season gets underway (Rollin, 1931) and singing activity is greatest in July (Rollin, 1931; Walpole-Bond, 1938; Clark, 1947). At this time average song length has been estimated as 2.7 minutes, although song-flights of as long as an hour have been observed (Rollin, 1931). There are opposing views about song behaviour during the incubation period. One report indicates that the males are relatively quiet when nests are being built and eggs incubated, and that song is resumed when the young are being fed (Clark, 1947). However, another report suggests that song-flight behaviour is at its greatest during incubation (Delius, 1963).

The birds tend to be quiet during August and September (perhaps while moulting) and between mid-November and mid-March (Rollin, 1931; Walpole-Bond, 1938; Clark, 1947).

In the breeding season the male skylarks ascend higher during their song-flights than at other times of year (Coward, 1925), to a height of about 100m (Suzuki *et al.*, 1952).

Although weather conditions may affect winter and autumn song behaviour, they generally have little effect in the breeding season (Clark, 1947). In fact, skylarks have been observed singing in a March snowstorm (Clark, 1947). However, the onset of singing activity at the beginning of the breeding season may be delayed by frost or snow. (Clark, 1947). Fog affects song behaviour at all times of year. In foggy conditions, the birds tend to sing in sight of the ground (Clark, 1947) and their song has a squealing note (Walpole-Bond, 1938).

There is little reference to the subject of the effect of time of day on song-flight behaviour in the literature, although one report suggests that frequency and length of song-flights do not vary with time of day (Delius, 1963).

5.4.1 Pilot study

Using this knowledge, a census walk method for estimating skylark breeding population density was investigated during the spring and summer of 1992. The estimation was based on counts of singing male skylarks made during walks along a 1.25km transect across Offham Farm, Lewes. This transect was chosen to follow existing paths and tracks, and designed to represent the types and the proportions of all crops and habitats on the farm.

It was assumed that each singing male skylark had a mate, was holding a territory and therefore represented a breeding pair. Singing larks that could be heard or seen without the aid of binoculars were counted. In most conditions birds could be heard singing up to 200 metres on either side of the transect path. It was important that birds could be heard as they were sometimes difficult to detect by sight alone. Although the birds could rise to a height of 100m metres or more (exact heights were difficult to estimate), no birds were heard that could not be seen with careful searching.

A population density of breeding skylark pairs was estimated by dividing the number of singing skylarks by the area of the transect:

$$\text{Pairs of skylarks/km}^2 = \frac{\text{number of singing males}}{\text{area of transect (ha)}} \times 100$$

5.4.2 Weather conditions and time of day

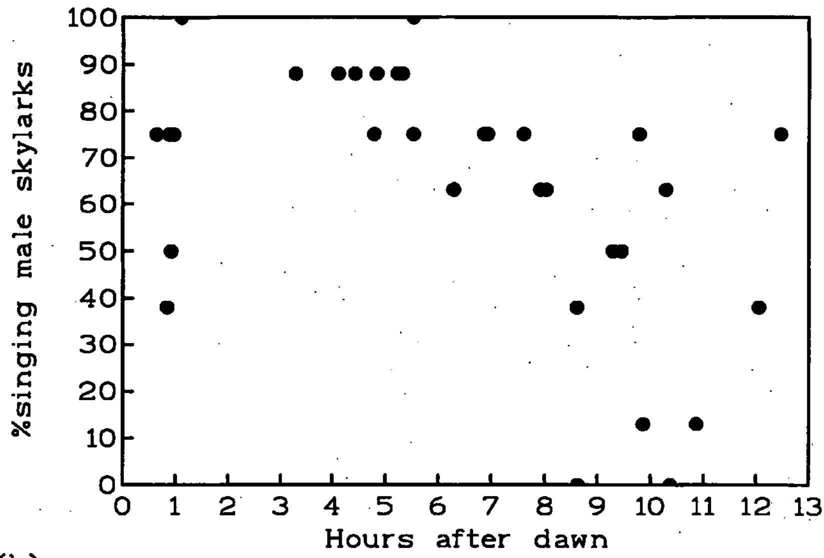
It was suggested that a transect method for estimating populations of breeding skylark pairs (described above) could be a reliable measure for comparing abundance between farms, provided that the effects of time of day, weather conditions and time in the breeding season on male song-flight behaviour were taken into account (John Marchant, personal communication). In order to investigate these effects the number of singing male skylarks counted along the 1.25km transect on Offham Farm was recorded on 32 occasions. These counts were made at different times of day (relative to sunrise) throughout April, May and June 1992 (breeding season 1992). Some of these counts were made on the same day, others on different days. Further data were collected from the same 1.25km transect the following year (breeding season 1993) to support these observations. This time, a series of 24 counts was made on one day (March 20). On this occasion, the first count was made at sunrise and, thereafter, subsequent counts were made every half hour until 1750. The investigations made on March 20 resulted in 30km of continuous walking (Appendix E).

There was no discernible relationship between song-flight behaviour and air temperature, atmospheric pressure or cloud cover. Generally, singing continued in rain, but it was not possible to tell if the birds were singing in heavy rain, as they could not be seen or heard. Therefore, counts were not made in very wet weather. For similar reasons counts were not made in foggy weather. It was not possible to count birds by sound alone in these conditions, as their behaviour seemed to change in fog (or at least their song was distorted) and it was difficult to tell how many birds were actually singing at a time. No particular change in song-flight behaviour was detected as the breeding season progressed. However, time of day did appear to influence song-flight behaviour (Fig 5.1a, for observations made in 1992, and Fig 5.1b, for the observations made in 1993).

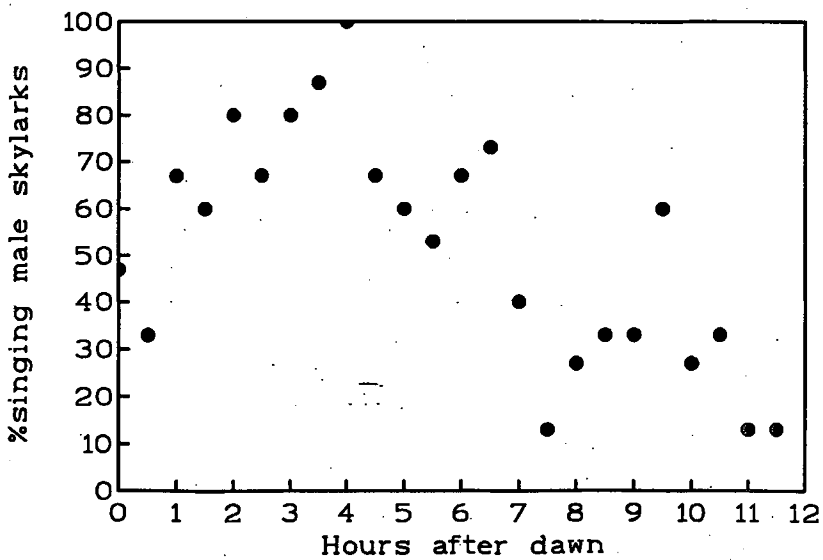
These graphs show that skylark singing activity rises to a peak in the morning and then declines as the day progresses. Counts should be made between two and six hours after dawn to give reliable and representative estimates of the number of breeding pairs along a transect. Counts made later in the day are less representative of the number of territory holding males, and also subject to greater variance in the number of males

Figure 5.1 **(a)** the percentage of skylarks singing along a transect across farmland at different times of day, on different days, throughout the 1992 breeding season, and **(b)** The percentage of skylarks singing along a transect across farmland at different times of day, on the same day (March 20) in the 1993 breeding season.

(a)



(b)



likely to be singing. This behaviour pattern is similar to that observed in other song bird species (Robbins, 1981), although it is at variance with the observations of Delius (1963), who reported that in his study area skylark song-flight behaviour did not vary with time of day.

5.4.3 Territory mapping

During the walks across Offham, to establish the reliability of the transect method for estimating breeding skylark density, some estimates of the locations of territories were made. A method similar to the CBC territory mapping system was used (see Marchant, 1983, for details of the method). On each walk along the transect the location of each of the singing skylarks present was recorded on a map. The information from each walk was then added together on one map, giving a rough outline of the territories held by different skylarks.

5.4.4 1992 survey

The results of the Offham Farm studies led to two counts being made along representative transects on the other study farms during the breeding season of 1992. First counts were made once on 16 farms and then a second count was made on 12 of these farms. Counts were always made within two to six hours after dawn and where possible commenced about four hours after dawn. The counts took, depending on farm size between one and three hours to complete. The first counts were made between April 15 and May 15, when pairs were attempting their first broods (referred to as first brood period), and the second counts were made between May 15 and June 15, when pairs were attempting a second brood or re-attempting a first brood (referred to as second brood period).

5.4.5 1993 survey

In the breeding season of 1993 the same transects were again walked on each of the 16 farms that had been studied in 1992. Although crop rotation caused some changes in the proportions of some habitat types between periods, on the whole the transects remained representative of the farms they crossed, and transects were only modified, where necessary, to include set-aside. In addition, one more farm, where hare survey work had been conducted, was included in the skylark investigation.

In 1993 two counts were made along each transect on 17 farms. The first of these (first brood period) were made between April 10 and May 1, and the second (second brood period) was made between May 15 and June 15. This allowed a count before and after May 1, the date at which legislation allowed farmers to cultivate or top rotational set-aside to control weeds. The location of wintering skylarks was recorded during field walks in the winter to map crop types.

5.4.6 Reliability of data

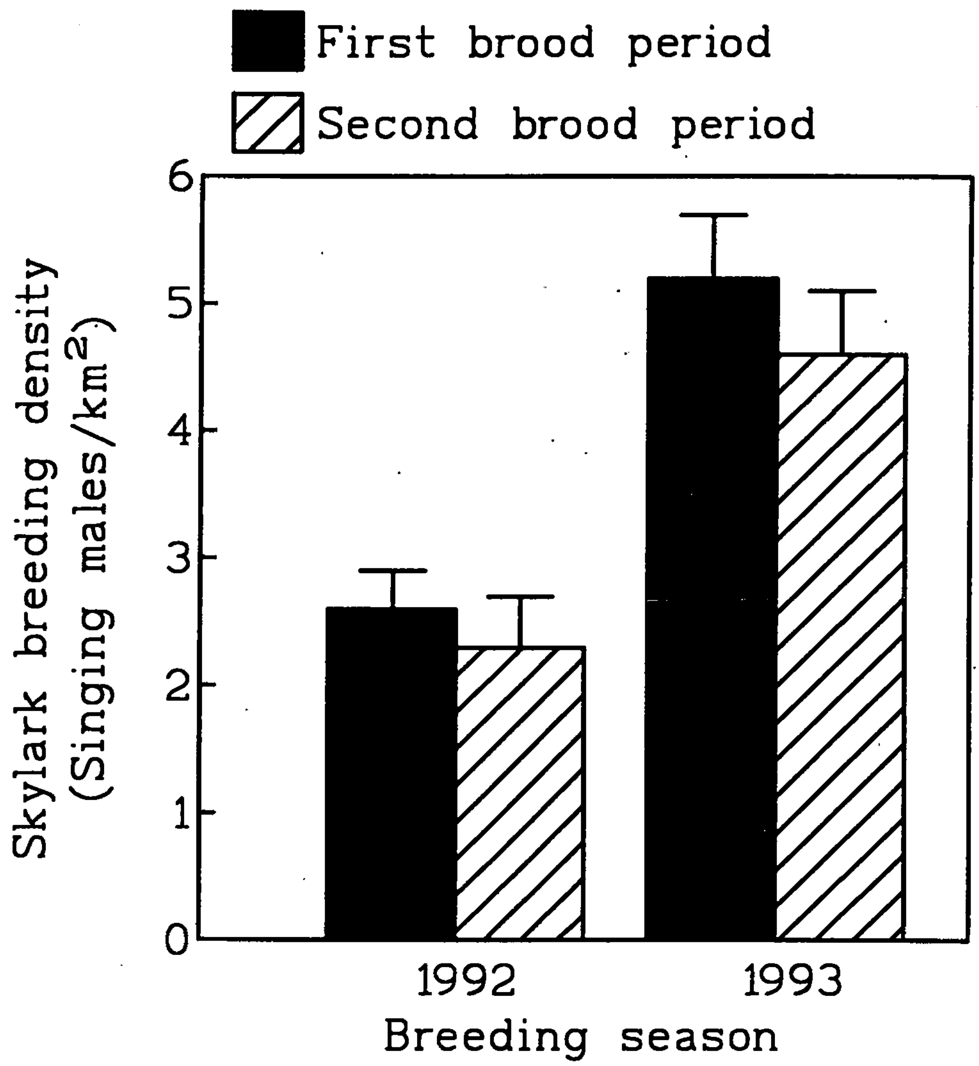
Unlike the hare study, the skylark study had no alternative sources of data on skylarks in the study area to back up the information collected from the transect walks. Although the study area farmers were aware of skylarks and could identify them when they were singing, most of those interviewed were not particularly interested in them and could provide no useful information about their numbers or behaviour. In addition, the majority of farmers did not have an opinion as to whether the population on their farm had changed over the last five years or longer periods of time. As skylarks are not currently a human food source, do not attract poachers onto farms and are not a crop pest on the South Downs, they do not receive much attention from farmers.

5.5 Results

5.5.1 Population trend

The results described in this chapter are based on analysis of data found in Appendix E. The average density of skylark breeding pairs over the whole area surveyed showed a big increase in numbers during the first two study years. There were approximately twice as many breeding pairs in the surveyed area in 1993 as in 1992 in both the first and second brood periods (Fig 5.2). Few wintering skylarks were seen. These were usually on stubble fields.

Figure 5.2 Skylark breeding pair abundance (mean numbers and standard errors of singing males/km^2 of farmland) in the 1992 and 1993 breeding seasons



5.5.2 Factors affecting nesting populations

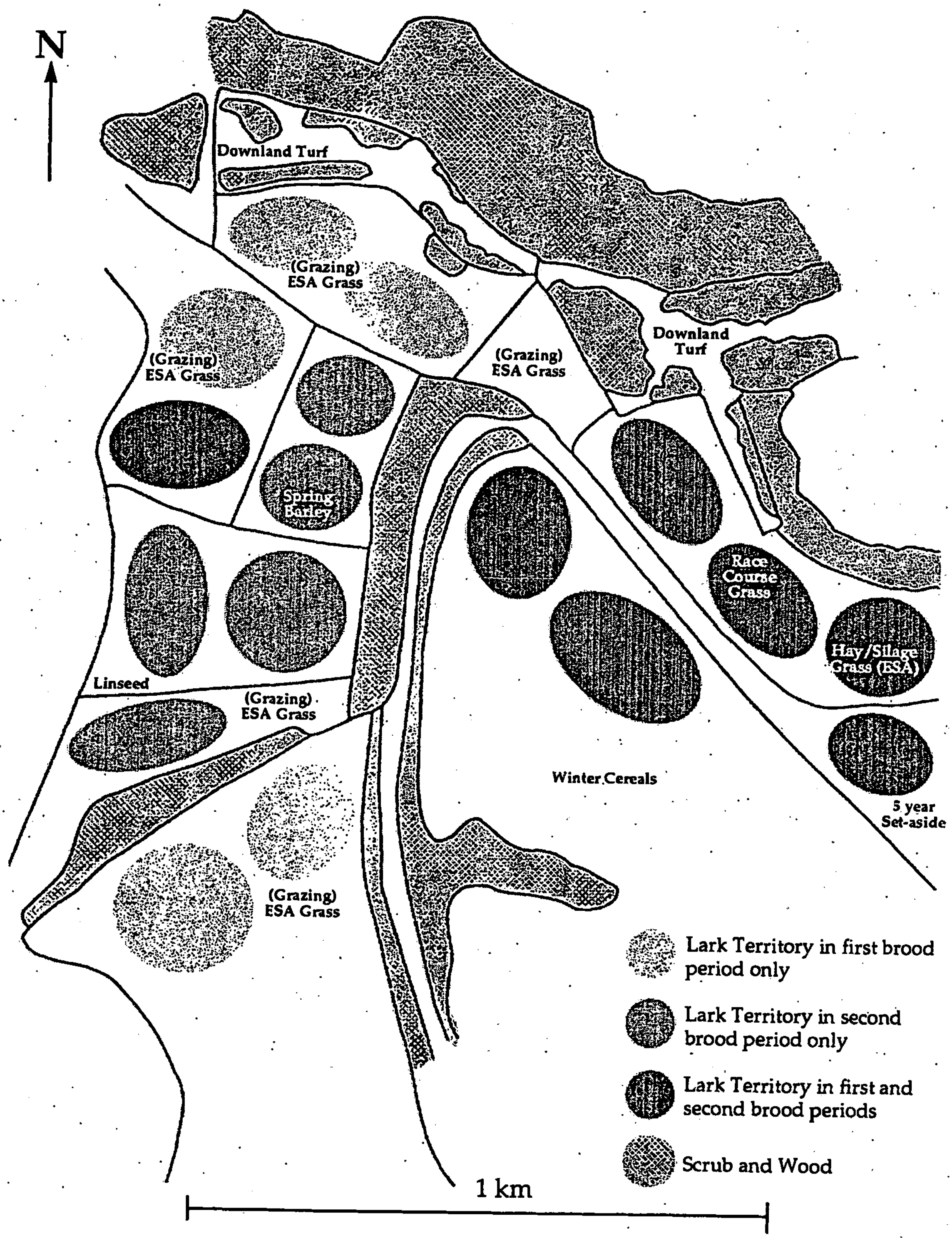
(a) Vegetation height

Skylarks tended to site their nesting territories in areas where the vegetation was between 15 and 25cm in height, and not too dense. This meant that woodland and scrub were avoided. Similarly, if the height of the vegetation was reduced below 15cm or grew up above 25cm while skylarks were using an area they tended to move and re-establish a new territory in vegetation which was within their preferred height range. Vegetation in this height range provides sufficient cover for the birds and their nests, and supports the invertebrates on which the chicks are fed (Poulsen and Sotherton, 1992), but it is not too tall for the skylarks to walk through (Schlapfer, 1988).

(b) Arable crops

As a result, in the first brood periods of 1991 and 1992 larks used winter sown arable crops for nesting, but avoided the recently sown and, therefore short, spring arable crops. In the second brood period they moved out of the winter arable crops as the crops grew too tall. They then established territories in spring arable crops which had by this time begun to grow. The movement of larks between crop types on Offham Farm is illustrated in Fig 5.3. This figure shows that the fields sown in the spring with linseed and barley on this farm, were not used by skylarks until the second brood period. This figure also

Figure 5.3 Location of skylark nesting territories on Offham Farm, 1992 breeding season



shows that skylarks held territories in the crop of winter wheat during both brood periods, which is unusual. The tendency for skylarks to move from winter sown arable crops to shorter spring sown crops between the first and second brood period is further illustrated in Figs 5.4a, for the 1992 breeding season, and 5.4b, for the 1993 breeding season, and summarised for both years in Table 5.1. These figures and table show the mean density of nesting pairs of skylarks in different crop types in first and second brood periods across the whole study area in the two survey periods. Analysis of variance was attempted to further investigate habitat use by the nesting larks, but limited data and a large number of variables meant that there were insufficient degrees of freedom to allow a meaningful interpretation of the results. The information in Fig 5.4a and Fig 5.4b can only be used as an indication of the nesting behaviour of the larks.

(c) Grassland

With the exception of four farms with dairy herds, much of the grassland (approximately 80%) in the study area was in the ESA scheme. As this could not be topped or mown until July 16, it provided suitable nesting habitat for the larks throughout both brood periods, provided it was not too heavily grazed. In addition, the larks using it tended to keep the same territories. This is illustrated for Offham Farm in Fig 5.3, which shows that ESA grass, which was heavily grazed by sheep, was generally deserted by the second brood period, but ESA grass which was kept for a hay or silage crop and therefore not grazed or mown until after July 16, was used by nesting skylarks in both the first and second brood periods.

Downland turf, which was often shorter than 5cm, and often associated with areas of scrub, was not a preferred nesting habitat in either brood period. This is illustrated in Fig 5.4a, for the 1992 breeding season, and Fig 5.4b, for the 1993 breeding season, and summarised for both years in Table 5.1. In the first brood period of 1992 no skylarks were observed holding territories over downland turf, although some territories were situated in downland turf in the second brood period. In 1993 downland turf was used for nesting by skylarks, but to a lesser extent than other habitat types.

Figure 5.4a Use of farmland habitats by nesting skylarks over the whole study area in the 1992 breeding season, indicated by mean numbers and standard errors of singing male skylarks/km^2 of each habitat type. KEY: WA, winter arable, GR, grass; SA, spring arable; DT, downland turf. There was only a very small area of set-aside in the study area in the 1992 breeding season.

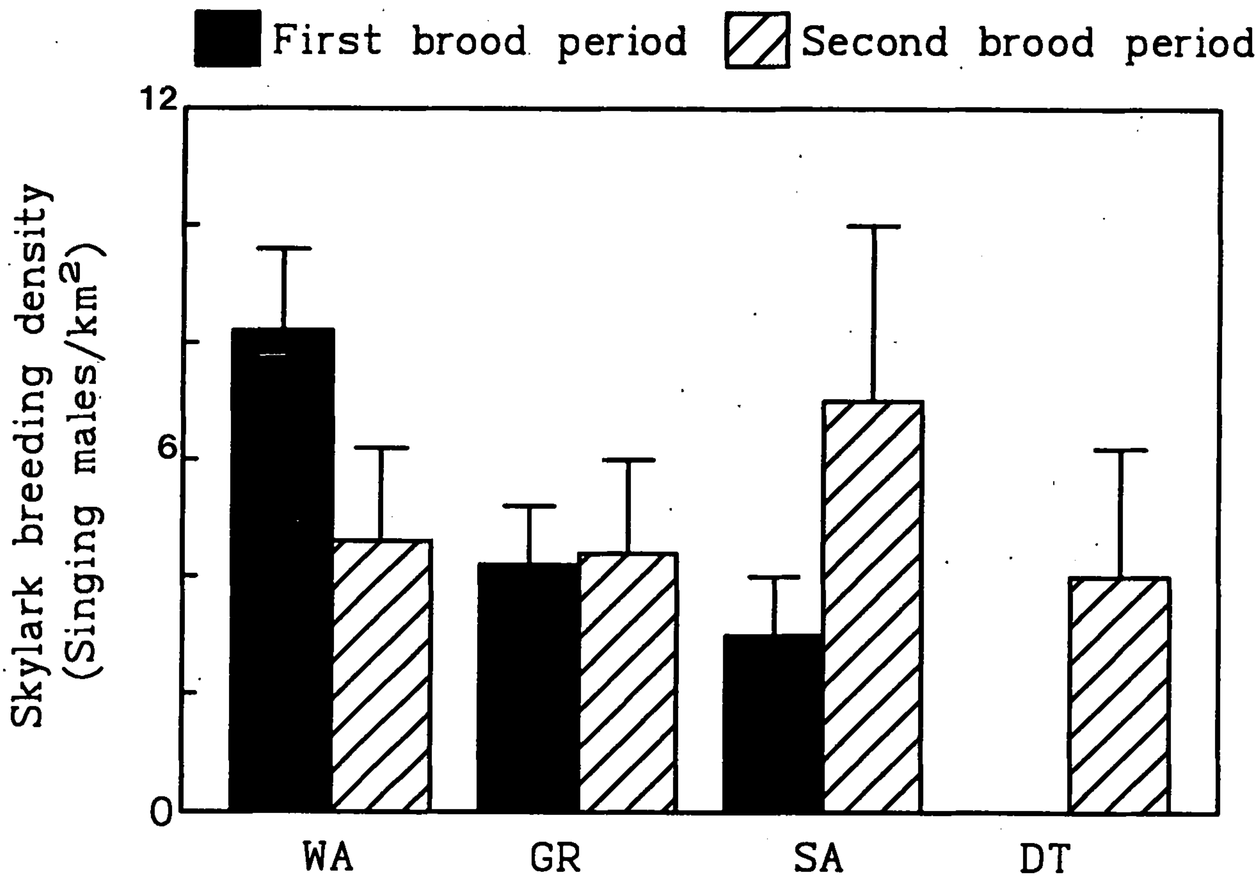


Figure 5.4b Use of farmland habitats by nesting skylarks over the whole study area in the 1993 breeding season, indicated by mean numbers and standard errors of singing male skylarks/km^2 of each habitat type. KEY: SS, set-aside; TS, topped set-aside; CS, cultivated set-aside; WA, winter arable, GR, grass; SA, spring arable; DT, downland turf.

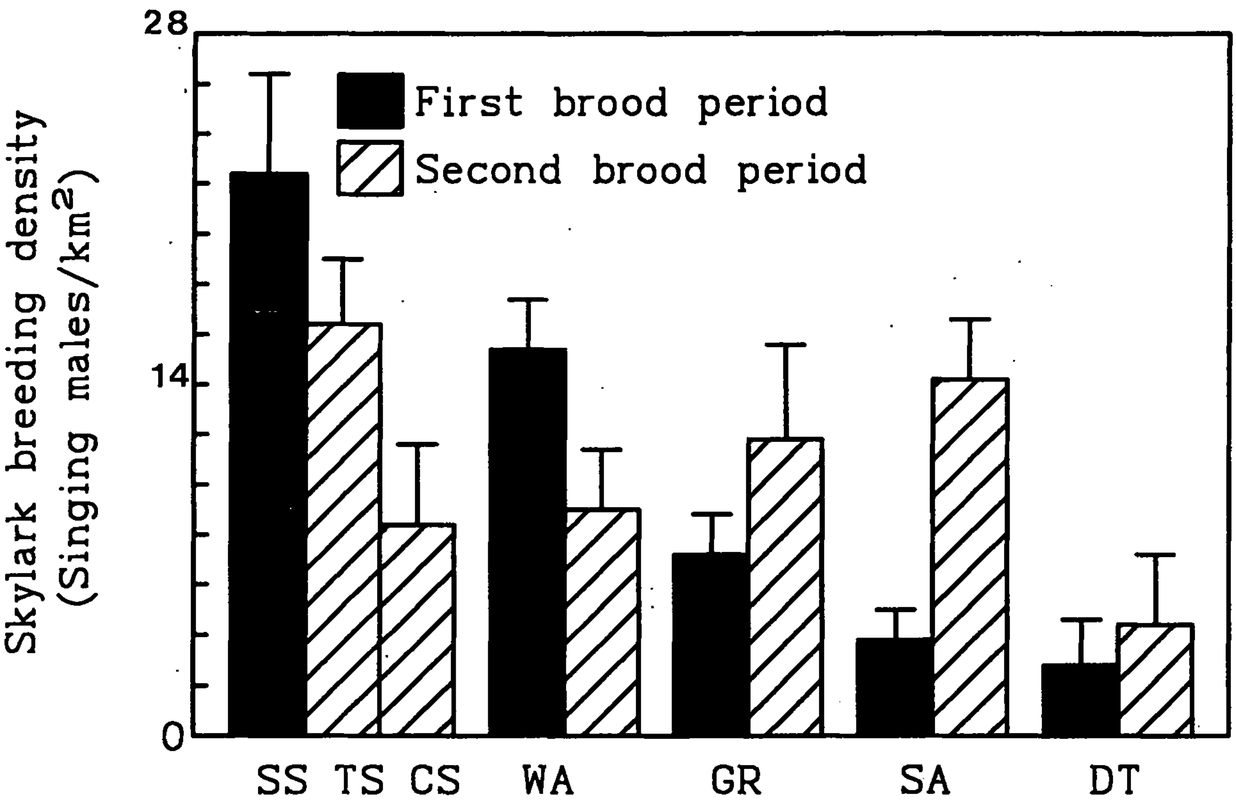


Table 5.1 Summary of the comparative use of farmland habitats by nesting skylarks. Key: WA, winter sown arable crops; SA, spring sown arable crops; SS, set-aside; TSS, topped set-aside; CSS, cultivated set-aside; GR, grassland; DT, downland turf. (1 indicates greatest use, 6 indicates least use).

	Comparative use					
	1	**2**	**3**	**4**	**5**	**6**
1992						
1st brood	WA	GR	SA	(DT not used)		
2nd brood	SA	WA	GR	DT		
1993						
1st brood	SS	WA	GR	SA	DT	
2nd brood	TSS	SA	GR	WA	CSS	DT

(Scrub and woodland not used in either year)

(d) Rotational set-aside

The only area of non-rotational set-aside in the study area during the 1992 breeding season was on Offham Farm (Fig 5.3). This provided perfect nesting conditions for skylarks and was used in both the first and second brood periods. The rotational set-aside scheme which was introduced at the end of 1992 also provided ideal nesting conditions. Singing male skylarks were up to six times as abundant on rotational set-aside land as on other habitat types in the first brood period. This is illustrated in Fig 5.4b, which shows the mean density of singing male skylarks in different habitat types over all 17 farms in the study area. The high density of skylarks was probably because the set-aside had not been sprayed and was providing cover and an abundance of invertebrate food species. In the second brood period topped set-aside was still a preferred habitat, but many territories on cultivated set-aside land were deserted. Young larks which could fly were observed to survive cultivation, but eggs and chicks in nests will have been destroyed. In the case of topped set-aside, nests may have survived topping but may then have been revealed to predators, as in a similar study by Poulsen and Sotherton (1993).

(e) Shelter

Results from subsequent related research indicate that skylarks position their territories in sheltered areas of fields, especially in very open downland (Wakeham-Dawson and Aebischer, unpublished data).

(f) Other farm enterprises and pesticide use

The density of singing male skylarks/km^2 of transect was estimated for each study farm during the first and second brood periods of 1992 and 1993. These results are illustrated in Fig 5.5a, for the 1992 breeding season, and 5.5b, for the 1993 breeding season. Analysis revealed no significant correlation between skylark density and farm habitat diversity (first brood period 1992, $F_{1,14} = 2.8$ NS; first brood period 1993, $F_{1,15} = 1.5$ NS), or any particular management practice on these farms. In the case of management practices, limited data and a large number of variables reduced the degrees of freedom necessary for a meaningful analysis of variance. However, from the results reported in the chapter on Brown hares, it can be seen that as hares have a relatively large range and will use the whole area of a farm, their population density can be related to particular farm management systems and the overall intensity of management on a particular farm. Perhaps the reason why skylark breeding density cannot be related, in a similar way, to overall farm management is because their choice of nesting territory is determined by more localised factors such as vegetation height, food availability or shelter from the prevailing wind.

It should be noted that although no clear trends can be shown over all the study farms, there were specific instances where skylark abundance on some farms was linked to specific management practices. For example, in 1992 (Fig 5.5a), nesting skylarks were particularly abundant on Farm O where there was a large area of ungrazed ESA grassland in the second brood period. Skylarks were also abundant during both the first and second brood periods

Figure 5.5a Density of nesting skylarks, indicated by the number of singing male skylarks/km^2, on each of 16 study farm in the first and second brood periods of the 1992 breeding season. Farms G, K, M and N were not surveyed in the second brood period.

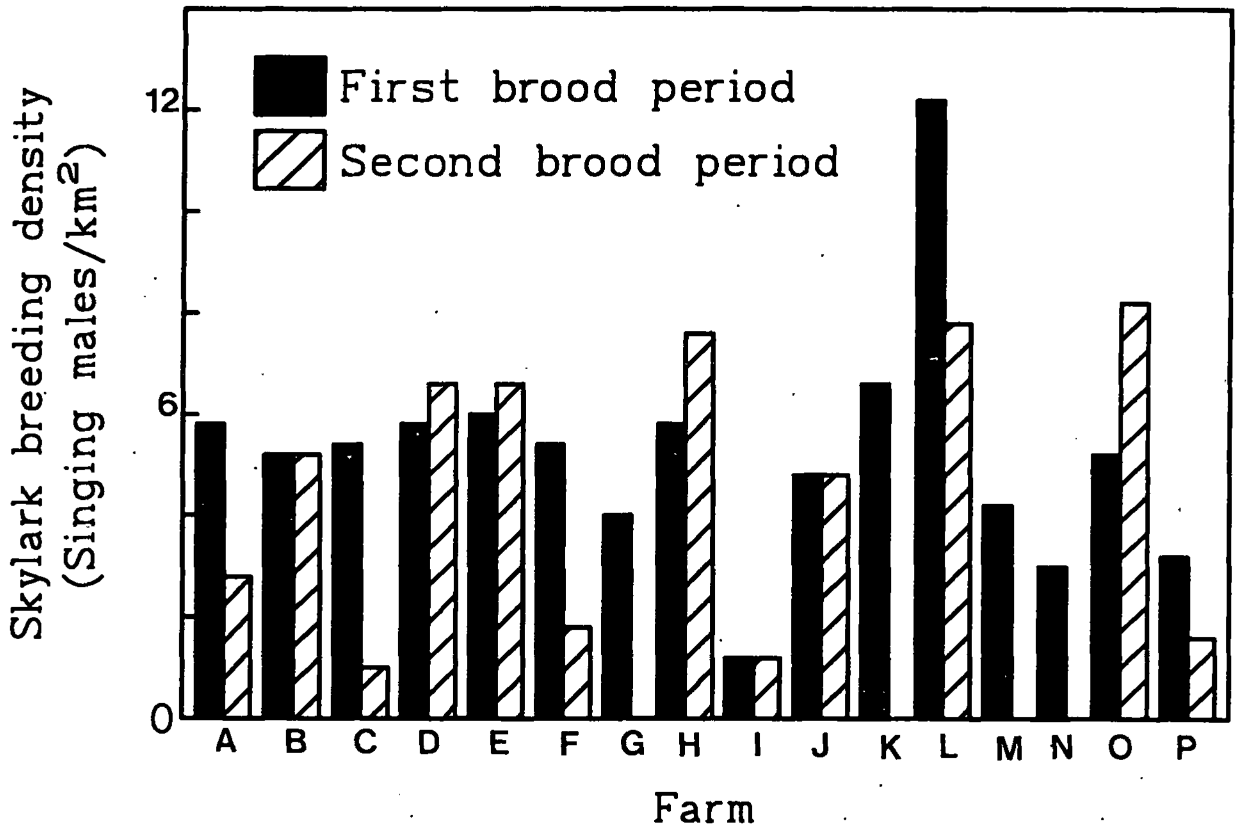
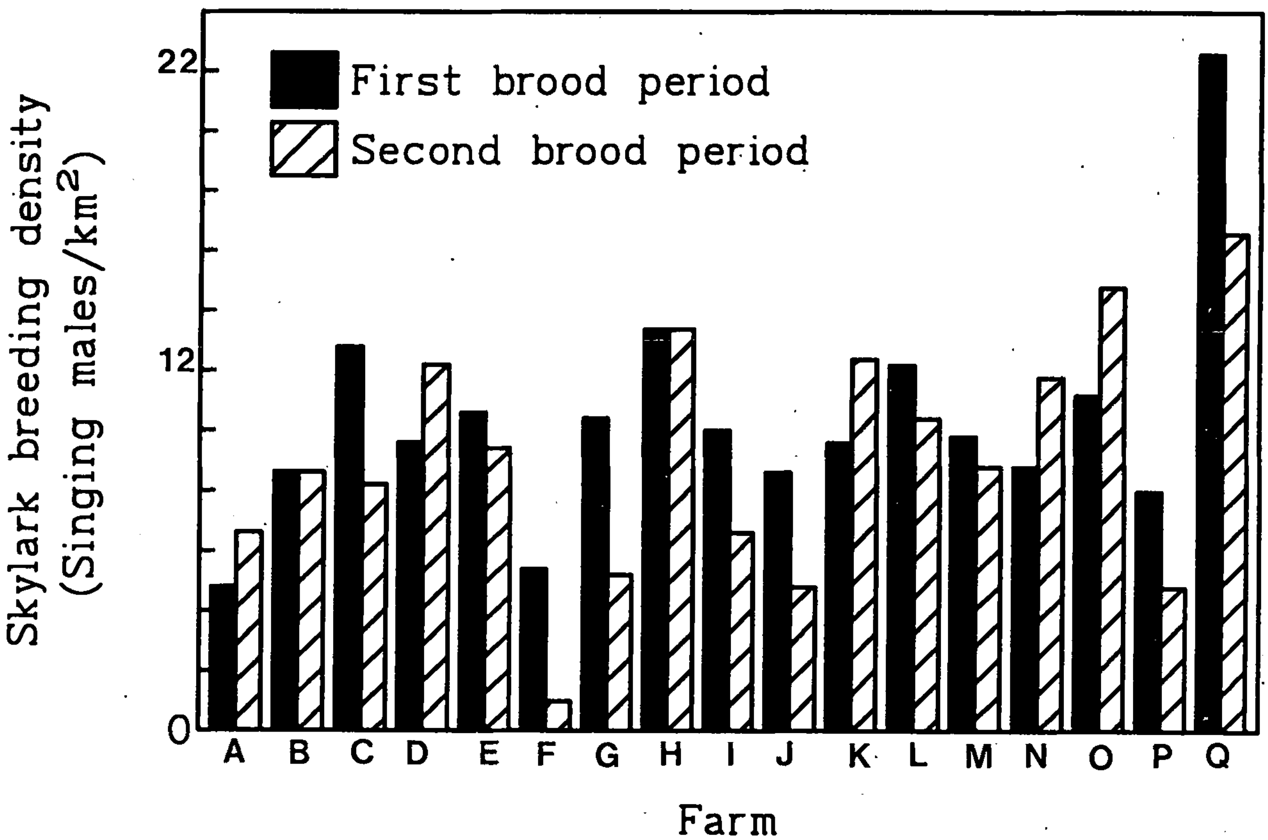


Figure 5.5b Density of nesting skylarks, indicated by the number of singing male skylarks/km^2, on each of 17 study farm in the first and second brood periods of the 1993 breeding season.



on Farm L, which had large areas of winter and spring sown arable. This was also still a particularly good farm for skylarks after whole farm reversion to ESA grassland, despite heavy grazing pressure. Conversely, nesting skylarks were less abundant during the second brood period on Farm C, as the whole farm was in winter wheat which had grown too tall, and on Farm F, as a large area of grass had been mown for silage.

In 1993 (Fig 5.5b), nesting skylarks were abundant on Farm C during the first brood period, as the whole farm was in rotational set-aside. However, by the second brood period the set-aside had been cultivated, making the farm less attractive to skylarks. Similarly, skylarks were abundant on Farm H during the first and second brood periods, as a large area of the farm was in rotational set-aside, which was not cultivated until after the farm was surveyed in the second brood period. Farm O had an abundance of skylarks in both brood periods because it provided a large area of under-grazed ESA. Skylarks were particularly abundant on Farm Q in both brood periods, because of the sensitive use of agricultural chemicals and the traditional ley-arable rotation system which are practised on this farm. Management of this nature probably encourages an abundance of invertebrate food species, which nesting skylarks can use for their chicks.

Skylark abundance was low, as it had been in 1992, on Farm F in the second brood period, as large areas were mown for silage. Skylark abundance was also low on Farm J in second brood period, as it had a large area of closely grazed ESA grassland.

From these specific instances, it would appear that rotational set-aside and ESA grassland can be beneficial to nesting skylarks if managed sensitively to keep vegetation at a suitable height to provide cover. In addition these schemes provide nesting habitats that are more suitable for skylarks than those available on areas subject to intensive mechanisation. These instances also suggest that the greatest density of nesting skylarks can be supported within a grass-arable rotation system where there is a sensitive use of agricultural pesticides. However, these conclusions are tentative and need further investigation.

(g) Predators

Few of the farmers interviewed could recall ever having found a skylark nest or having found any damaged nests. During the current research, crows were often observed foraging on grassland where skylarks were nesting, but analysis did not reveal any correlation between predator control and lark abundance. Gamekeepers control crows and magpies which are both predators of skylark eggs and nestlings. It is possible that the effects of predation on skylarks can only be revealed by a study of breeding success. Perhaps breeding success is greater on farms where corvid predators were controlled, even though the abundance of larks attempting to breed, albeit less successfully, is not affected.

5.5.3 Summary of results

The abundance of nesting skylarks in the study area was controlled mainly by localised factors which affected the availability of suitable nesting territories. Habitat types that provided suitable nesting cover and, presumably food for adults and chicks, supported denser nesting populations. The birds tended to move territories if vegetation grew too tall or was grazed or mown very short. There was no significant correlation between any particular farm management practice or farm habitat diversity over the whole study area, but breeding skylark density tended to be lower on areas of farms where there was intensive stocking or silage making.

The introduction of rotational set-aside was generally beneficial to skylarks as it provided good nesting territory, but topping activities may have resulted in the loss of nests and broods. The introduction of ESA grassland was beneficial to skylarks if not grazed too intensively.

The implications of these findings for the use of the skylark as an indicator species in monitoring environmental change will be discussed in the final chapter (Chapter 6).

Chapter 6 Summary and Conclusions

6.1 Hares, skylarks and modern agriculture

The results of the current research, and related research reviewed in this thesis:

(1) suggest that populations of both hares and skylarks are affected by the management practices farmers adopt.

(2) provide examples, albeit in some cases anecdotal, of the ways in which crop type and crop rotation systems, timing of field operations, use of machinery, grazing management, and the use of agricultural chemicals on farms may affect the ecology of both species.

(3) indicate that environmentally sensitive farming practices can be beneficial to both species.

6.2 Hares, skylarks and environmentally sensitive agriculture

It is important to note, however, that legislation designed to encourage less intensive and more environmentally sensitive agriculture is not automatically beneficial to all wildlife. While rotational set-aside is potentially a good habitat type for hares and skylarks, the ways in which farmers are encouraged to manage it need modifying before benefits to wildlife are optimised. For example, the timing and methods of weed control on set-aside need to be reviewed to prevent set-aside becoming a wildlife 'ambush'. Hares and skylarks attracted onto the set-aside land can be killed or revealed to predators by the ploughing or topping operations required as a condition of set-aside payment (Poulsen and Sotherton, 1993). However, it should be noted that some modifications have already been made since the start of the current study, allowing farmers to use pesticides that will kill weeds but leave cover for animals using the set-aside (MAFF, 1993).

The current research suggests that Environmentally Sensitive Area (ESA) grassland, as yet, appears to be far from satisfactory for either hares or skylarks. This is especially the case where large areas of farms have been placed in the scheme and livestock are allowed to roam freely, making the whole area unattractive to hares. Although undergrazed ESA provides good nesting cover for skylarks, the birds avoid fields where the grass is grazed very tightly. As MAFF recommends that ESA grass is kept below 10 cm in height, current ESA management recommendations are unlikely to favour skylarks if adhered to closely. Further research which is now being undertaken by the Game Conservancy Trust for MAFF, leading on from the current research, is investigating ways of optimising ESA grassland as farmland bird habitat. The new research will be investigating aspects of ESA management such as the seeds mixtures sown and the ways in which the grassland is grazed.

Research reviewed in this thesis suggests that hares and skylarks thrive best on farms where there is a mixed grass and arable rotation. These conditions ensure that weed plants and invertebrate life can flourish and, in so doing, provide food for wildlife (Sotherton, 1992: Aebischer, 1993). Perhaps legislation to encourage more environmentally sensitive agriculture would be of greater value to species such as hares and skylarks if aimed at generally reducing the intensity of production within traditional arable rotation systems, rather than by entering large areas of downland to grass. For example, winter stubbles and rotational set-aside which are so attractive to nesting skylarks and hares feeding in the winter, are a product of an arable system. These are lost when large areas of downland are converted from arable to ESA grass. Although, setting aside some areas of farmland may result in a continuation or intensification of management which can be unfavourable to wildlife on the areas remaining in production. However, the new area payment scheme for arable support introduced in 1992, which accompanies the set-aside policy, may be influential in reducing the intensity of mechanical and chemical use on farmland, as it discourages high input-high yield production systems. This is because the new scheme, unlike its predecessors, makes arable support payments to farmers on the basis of production area, rather than of yield.

The conservation of existing downland turf and the creation of new areas of downland turf are important management aims. However, many of the fields being put into arable reversion may not have the specialised environmental conditions (such as very shallow, nutrient-poor soils) to allow downland turf to develop, especially if sown with rye grass and white clover. In these areas, current ESA management recommendations are producing a species-poor grassland monoculture of low value for wildlife conservation and of no value to agriculture. This grassland monoculture may match an idyllic view of how the South Downs once were, but (as discussed in Chapter 1) history provides no evidence that the South Downs were ever a grassland monoculture. Although it is true that the balance between grassland and arable has been in a state of constant flux over the centuries and the area of grassland has been greater at some times than others, there has always been a mixture of arable crops and grassland. It is to this mixture that many downland wildlife species are adapted.

Certain areas which are likely to revert to true downland turf should perhaps be targeted and managed accordingly. The remaining areas should be managed differently to optimise their value to farmland birds and other forms of wildlife, which like the chalk grassland itself, have adapted over the last six thousand years or more to a cultivated agricultural ecosystem. The answer, though an unconventional approach, would be to modify the ESA schemes to incorporate some low-input arable production options. For example, spring-sown arable crops could provide nesting habitat not only for the species which currently nest in downland, but for other species such as lapwing and stone curlew (*Burhinus oedicnemus*) which have become increasingly rare (Marchant *et al.*, 1990). Inclusion of low-input arable production options in the ESA schemes would also ensure the conservation of rare arable wildflowers that grow on light soils and cannot survive in a competitive, permanent grass sward (Wilson and Sotherton, 1994). Inclusion of arable options in the downland ESA schemes would also ensure that sufficient sheep could be supported on farms to provide the intensive grazing that true areas of downland turf require (Paul Wakeham-Dawson, personal communication).

6.3 Hares and skylarks as indicators

Indicator potential value (IPV). How in practice did hares and skylarks fulfil the criteria which were used to select them as potential indicators in Chapter 2?

Nine criteria were used to select vertebrate indicators for this study. The aim of the selection procedure was to identify downland species (1) whose ecology was well understood, (2) which were not affected by regular population cycles or other factors unconnected from the impact of the factors being studied, (3) which were adapted to agricultural ecosystems, (4) which were habitat generalists, (5) which were abundant, (6) which were not farmed or (7) controlled as a pest, (8) which were easy to study, and (9) which were resident within the study area.

Both species satisfied Criteria 3, 5, 6 and 8 in a manner that the initial literature review had suggested they might, and in retrospect, the exclusion of criterion 1 from the selection process is justifiable in that the ecology of all the species originally listed is well understood. In particular, the considerable information available on hares and skylarks is illustrated by the literature reviews in Chapters 4 and 5. However, in the other criteria there were some differences in the way the initial literature review had suggested hares and skylarks could act as indicators and the eventual findings of this research. In particular, the present study reinforced an understanding of the large effect of predator control on hare ecology. As predator control can over-ride the effects of other ecological factors on hares, it weakens their potential as indicators of the effects of agricultural management practices (criterion 2), unless it is specifically taken into account. An additional criterion, which states that species affected by predator control are unlikely to make ideal indicators, should be added to the selection procedure for identifying potential indicator species. This study did not provide conclusive information on the effects of predator control on skylarks. The study reinforced the evidence that skylarks avoid scrub and woodland and are not habitat generalists (criterion 4). It showed that they also avoid downland turf. As downland turf is an important habitat type in the downland ecosystem and its re-establishment is an aim of some environmentally sensitive grant schemes, this weakens the indicator value of skylarks and their use in monitoring the beneficial outcomes of such schemes. But it does re-inforce that species like skylarks are adapted to open arable land and *not* downland turf, the habitat type which current ESA management is attempting to create. On the whole hares were not shot as pests, but in cases where they were, their indicator value was reduced. The effects of undetected poaching also reduces their indicator value. Although hares were observed to be resident on the study area all year around, very few skylarks appeared to be present in the winter. This reduces the indicator value of the skylarks, as they will have been affected by factors outside the study area during the winter (criterion 9).

Despite these limitations, the current research has shown that brown hares can be used to provide an indication of the intensity of management over whole farms. This is probably because hares tend to use a relatively large home range. Nesting skylarks, however, have a relatively small territory, and where they chose to hold a territory is influenced by very local factors at field level. For this reason, counts of nesting skylarks made along transects cannot be correlated with global farm management. However, skylarks can be used to assess the effects of management practices within specific crop types. This is well illustrated by the way skylarks respond to grazing intensity and set-aside management.

Measuring the response of hare and skylark populations to the introduction of new management schemes obviously indicates the effects of environmentally sensitive legislation on the species themselves. But to what degree are their responses representative of the ways in which other vertebrate species in the downland ecosystem are affected? To some extent this is still speculative and cannot be fully answered from the results of the current research. However, there is good evidence from the current study itself and from other sources within the study area to support the view that other downland vertebrates respond to farm management practices in similar ways to hares and skylarks. For example, Applesham Farm (Q), where hare and skylark populations thrive, supports an abundance of grey-partridges and corn buntings (Dr Dick Potts, personal communication; Rebecca Ward, personal communication; Wakeham-Dawson & Aebischer, unpublished data). It appears that all these ground-nesting bird species benefit from the traditional ley-arable rotation and sensitive use of agricultural chemicals that are practised on this farm.

The results of the current research suggest that the use of indicators such as hares and skylarks has great potential for monitoring in the downland ecosystem. This potential could be further enhanced by (1) the use of a number of indicator species which could represent environmental changes within all the habitat components of the downland, (2) an assessment of changes in productivity and breeding success of indicator species to accompany investigations of abundance (Van Horne, 1983); this could reveal responses to more environmentally sensitive farming that are not indicated by changes in adult abundance alone, and (3) experiments to quantify why some areas of farms are favoured by the chosen indicator species. In particular this should include an investigation of floral and invertebrate diversity, as these organisms provide food for vertebrates.

6.4 Conclusion

Hares and skylarks are easy species to survey. Both species can be affected by the ways farmers manage their land. With careful management environmentally sensitive farming schemes in the South Downs could favour both species. Encouraging farming practices that favour these species is a worthwhile aim in itself. In addition, if further research supports the evidence provided tentatively here that their response to farm management practices is indicative of the response of other species, census of these species would be a valuable component of monitoring in the downland ecosystem. Their study would complement the monitoring of botanical species for which MAFF is responsible in the South Downs ESA.

References

Abildgård, F., Andersen, J. & Barndorff-Nielsen, O. (1972). The hare population (*Lepus europaeus* Pallas) of Illume Island, Denmark. A report on the analysis of the data from 1957-1970. *Danish Review of Game Biology* **6**:1-32.

Aebischer, N. (1993). The Sussex study: 23 years of monitoring. *The Game Conservancy Review of 1992*, 53-55. Fordingbridge: The Game Conservancy Trust.

Andersen, J. (1952). Fluctuations in the field hare population in Denmark compared with certain climatic factors. *Papers Game Research* **8**:41-43.

Andersen, J. (1957). Studies in Danish hare populations I: population fluctuations. *Danish Review of Game Biology* **3**: 85-131.

Andrzejewski, R. & Jezierski, W. (1966). Studies on the European Hare XI. Estimation of population density and attempt to plan the yearly take of hares. *Acta Theriologica* **11**: 433-448.

Andrzejewski, R. & Pucek, Z. (1965). Studies on the European Hare X: Results so far obtained from research in Poland and trends in continued studies. *Acta Theriologica* **10**: 79-91.

Anscombe, F. J. (1948). The transformation of Poisson, binomial, and negative-binomial data. *Biometrika* **35**: 246-254.

Arnold, H. R. (1978). (Ed.) *Provisional Atlas of the Mammals of the British Isles.* Monks Wood, Institute of Terrestrial Ecology.

Barnes, R. F. W. & Tapper, S. C. (1985). A method for counting hares by spotlight. *Journal of Zoology* **206**: 273-276.

Barnes, R. F. W., Tapper, S. C. & Williams, J. (1983). Use of pastures by brown hares. *Journal of Animal Ecology* **20**: 179-185.

Barnes, R.F.W. & Tapper, S.C. (1986). Consequences of the myxomatosis epidemic in Britain's rabbit (*Oryctolagus cuniculus* L.) population on the numbers of brown hares (*Lepus europaeus* Pallas). *Mammal Review* **16**: 111-116.

Bibby, C. J. & Burgess, N. D. & Hill, D.A. (1992) *Bird Census Techniques.* London: Academic Press.

Binns, J. A., Funnell, D. C. & Stephens, A. G. (1993). *Agricultural Change in Sussex.* Brighton: University of Sussex.

Bliss, C. L. & Fisher, R. A. (1953). Fitting the negative binomial distribution to biological data. Note on the efficient fitting of the negative binomial. *Biometrics* **9**: 176-200.

Botkin, D.B., Woodby, D.A. & Nisbet, R.A. (1991). Kirtland's warbler habitats: a possible indicator of climatic warming. *Biological Conservation* **56**: 63-78.

Bresinski, W. & Chlewski, A. (1976). Tree stands in fields and spatial distribution of hare populations. In *Ecology and Management of European Hare Populations*, 185-193 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Bresinski, W. (1976a). Weather conditions vs European hare population dynamics. In *Ecology and Management of European Hare Populations*, 105-114 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Bresinski, W. (1976b). Agrarian Structure vs the European Hare Population Density. In *Ecology and Management of European Hare Populations*, 195-197 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

British Ecological Society (1990). *Ecological Issues 1: Riverwater Quality*. London, BES.

Brockless, M. & Tapper, S. C. (1993). Small mammals on Loddington set-aside. *The Game Conservancy Review of 1992*, 47-48. Fordingbridge: The Game Conservancy Trust.

Broekhuizen, S. (1975). The position of the wild rabbit in the life system of the European hare. *XII Congresso da Uniao Internacional dos Biologists da Caca*: 75-79.

Broekhuizen, S. (1976). The situation of hare populations in the Netherlands. In *Ecology and Management of European Hare*

Populations, 23-24 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Broekhuizen, S. (1979). Survival in adult European hares. *Acta Theriologica* 24: 465-473.

Broekhuizen, & S. Kemmers, R. (1976). The stomach worm, *Graphidium strigosum* (Dujardin) Railliet & Henry, in the European hare, *Lepus europaeus* Pallas. In *Ecology and Management of European Hare Populations*, 157-171 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Broekhuizen, S. & Maaskamp, F. (1981). Annual production of young in European hares (*Lepus europaeus*) in the Netherlands. *Journal of Zoology* **193**: 499-516.

Broekhuizen, S. & Maaskamp, F. (1982) Movement, home range and clustering in the European hare (*Lepus europaeus* Pallas) in the Netherlands. *Journal of Zoology* **195**: 22-32.

Broekhuizen, S. & Maaskamp, F. (1976). Behaviour and maternal relations of young European hares during the nursing period. In *Ecology and Management of European Hare Populations*, 59-67 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Broekhuizen, S. & Maaskamp, F. (1980). Behaviour of does and leverets of the European Hare (*Lepus europaeus*) whilst nursing. *Journal of Zoology* **191**: 487-501.

Brown, D. (1991). Killer virus steals a march on hares. *The Times*, 9 January 1991.

Busche, G. (1989). [Drastic decrease in the population of the skylark, *Alauda arvensis*, in pastures and meadows in Schleswig-Holstein, FRG.] *Die Vogelwelt Jg*. **110**: 51-59.

Cairns, J. (1986). The myth of the most sensitive species. *Bioscience* **36**: 670-672.

Carr, S. (1988). Conservation on Farms: Conflicting Attitudes, Social Pressures and Behaviour. PhD. Thesis, The Open University.

Carson, R. (1962). *Silent Spring*. New York, Hamish Hamilton.

Chlewski, A. (1976). Estimation of the degree of danger to the European hare caused by pesticides. In *Ecology and Management of European Hare Populations*, 231-236 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Clark, R. B. (1947). Seasonal fluctuations in the song of the sky-lark. *British Birds* **40**: 34-43.

Clutton-Brock, J. (1989). Five thousand years of livestock in Britain. *Biological Journal of the Linnean Society* **38**: 31-37.

COM/91/100. Proposals of the Commission. *Commission of the European Communities*. Brussels, 1 February 1991.

COM/91/258. The development and the future of the Common Agricultural Policy. *Commission of the European Communities.* Brussels, 11 July 1991. Communication of the Commission to the Council and to the European Parliament.

COM/91/379. Reforms of the Common Agricultural Policy. *Commission of the European Communities.* Brussels, 18 October 1991.

Corbet G.B. (1986) Relationships and origins of the European Lagomorphs. *Mammal Review* **16**: 105-110.

Corbet G.B. & Harris, S. (1991). *The Handbook of British Mammals.* London: Blackwell Scientific Publications.

Coward, T. A. (1925). *The Birds of the British Isles and their Eggs.* London: Warne.

Croxall, J. P., McCann, T. S., Prince, P. A. & Rothery, P. (1988). Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976-1987: implications for monitoring studies. In *Antarctic Ocean and Resources Variability* (Ed. D.Sahrhage). Berlin: Springer-Verlag.

Curwen, E. C. (1930). *Prehistoric Sussex.* The Homeland Association, London.

Delius, J. D. (1963). Das verhalten der feldlerche. *Z. Tierpsychol* **20**: 297-348.

Delius, J. D. (1965). A population study of skylarks *Alauda arvensis*. *Ibis* **107**: 466-492.

Dzilinski, E. & Chlewski, A. (1976). Estimated residues of polychloric insecticides in the fatty tissues of the European hare. In *Ecology and Management of European Hare Populations*, 213-217 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

EEC (1985). Council Regulation (EEC) No. 797/85 of 12 March 1985 on improving the efficiency of agricultural systems. *Official Journal of the European Communities* **28**: 1-18.

EEC (1987). Council Regulation (EEC) No. 1760/87 of 15 June 1987 amending Regulations (EEC) No. 797/85, (EEC) No. 270/79, (EEC) No. 1360/78 and (EEC) No. 355/77 as regards agricultural structures, the adjustment of agriculture to the new market situation and the preservation of the countryside. *Official Journal of the European Communities* **30**: 1-8.

EEC (1988). Commission Regulation (EEC) No. 4115/88 of 21 December 1988 laying down detailed rules for applying the aid scheme to promote the extensification of production. *Official Journal of the European Communities* **31**: 13-18.

Eltringham, S.K. & Flux, J.E.C. (1971). Night counts of hares and other animals in East Africa. *East African Wildlife Journal*. **9**: 67-72.

Erhardt, A. (1985). Diurnal lepidoptera: sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology* **22**: 849-861.

Everett, R. D. (1979). The functions of wildlife and their possible use for deriving site selection components. *Biological Conservation* **13**: 207-218.

Flux, J.E.C. (1965). Timing of the breeding season in the hare, *Lepus europaeus* Pallas, and the rabbit, *Oryctalagus cuniculus* L. *Mammalia* **29**: 557-562.

Flux, J.E.C. (1967). Reproduction and body weights of the hare, *Lepus europaeus* Pallas, in New Zealand. *New Zealand Journal of Science* **10**: 357-401.

Flux, J.E.C. (1981). Field observations of behaviour in the Genus *Lepus*. *Proceedings of the World Lagomorph Conference 1979*, 377-394 (Ed. by K. Myers & C.D. MacInnes). Ontario: University of Guelph.

Frylestam, B. (1976a). The European hare in Sweden. In *Ecology and Management of European Hare Populations*, 33-34 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Frylestam, B. (1976b). Effects of cattle-grazing and harvesting of hay on density and distribution of an European hare Population. In *Ecology and Management of European Hare*

Populations, 199-203 (Eds Z. Pielowski and Z.Pucek). Warsaw, Polish Hunting Association.

Frylestam, B (1980a). Reproduction in the European hare in southern Sweden. *Holarctic Ecology* **3**: 74-80.

Frylestam, B (1980b). Growth and body weight of European hares in southern Sweden. *Holarctic Ecology* **3**: 81-86.

Frylestam, B. (1981). Estimating by spotlight the population density of the European hare. *Acta Theriologica* **26**: 419-427.

Frylestam, B. (1986). Agricultural land use effects on the winter diet of Brown hares (*Lepus europaeus* Pallas) in southern Sweden. *Mammal Review* **16**: 157-161.

Game Conservancy (1991). *The Game Conservancy Review of 1990*, 33. Fordingbridge: The Game Conservancy Trust.

Game Conservancy (1992). *The Game Conservancy Review of 1991*, 40. Fordingbridge: The Game Conservancy Trust.

Gause, G. F. (1964). *The Struggle for Existence*. Baltimore: Williams and Wilkins.

Gehlbach, F. R. (1975). Investigation, evaluation, and priority ranking of natural areas. *Biological Conservation* **8**: 79-88.

Goldsmith, F. B. (1975). The evaluation of ecological resources in the countryside for conservation purposes. *Biological Conservation* **8**: 89-96.

Goszczynski, J. Ryszkowski, L. & Truszkowski, J. (1976). The role of the European hare in the diet of predators in cultivated field systems. In *Ecology and Management of European Hare Populations*, 127-133 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Green, B. H. (1989). Agricultural impacts on the rural environment. *Journal of Applied Ecology* **26**: 793-802.

Green, R. (1987). Factors affecting the diet of farmland skylarks, *Alauda arvensis*. *Journal of Animal Ecology* **47**: 913-928.

Green, R. E. (1980). Food selection by skylarks and grazing damage to sugar beet seedlings. *Journal of Applied Ecology* **17**: 613-630.

Grinnell, J. (1924). Geography and evolution. *Ecology* **5**: 225-229.

Haigh, N. (1987). *EEC Environmental Policy and Britain*. London: Longman.

Hardman, J. A. (1974). Biology of the skylark. *Annals of Applied Biology* **76**: 337-341.

Hawksworth, D. L. & Rose, F. (1976). *Lichens as Pollution Monitors*. Studies in Biology No. 66. London: Arnold.

Hellawell, J. M. (1978). *Biological Surveillance of Rivers: a Biological Monitoring Handbook*. Stevenage: Water Research Centre.

Hellawell, J. M. (1986). *Biological Indicators of Freshwater Pollution and Environmental Management*. London: Elsevier.

Helliwell, D. R. (1987). Survey and evaluation of wildlife on farmland in Britain: an 'indicator species' approach. *Biological Conservation* **13**: 63-73.

Henderson, A. C. B. (1979). *Survey of Semi-natural Grassland of the South Downs in East Sussex 1978-1979*. English Nature, Lewes, Sussex.

Hewson, R. (1963). Moults and pelages in the brown hare, *Lepus europaeus occidentalis* de Winton. *Proceedings of the Zoological Society of London* **141**: 677-688

Hewson, R. (1977). Food selection by brown hares (*Lepus capensis*) on cereal and turnip crops in North-east Scotland. *Journal of Applied Ecology* **14**: 779-785.

Hewson, R. & Taylor, M. (1975). Embryo counts and length of breeding season in European hares shot from 1900-1972. *Acta Theriologica* **20**: 247-254.

Holley A. J. F. (1986). A hierarchy of hares: dominance status and access to oestrous does. *Mammal Review* **16**: 181-186.

Hudson, W. H. (1923). *Nature in Downland.* Dent, London.

Ibery, B. (1992). *Agricultural Change in Great Britain.* Oxford: University Press.

Jenny, M. (1990). Territorialitat und brutbiologie der feldlerche *Alauda arvensis* in einer intensiv genutzten agrarlandschaft. *Journal fur Ornithologie* **131**: 241-265.

Kadulski, S. & Dobrynczuk, J. (1976). Observations on the ecto-parasites of the European hare. In *Ecology and Management of European Hare Populations*, 177-183 (Eds Z. Pielowski and Z.Pucek). Warsaw, Polish Hunting Association.

Kaluzinski, J. and Pielowski, Z. (1976). The effect of technical agricultural operations on the hare population. In *Ecology and Management of European Hare Populations*, 205-211 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Keith, L.B. (1981). Population dynamics of hares. In *Proceedings of the World Lagomorph Conference*, 395-440 (Eds K. Myers and C.D. MacInnes). Ontario: University of Guelph.

King, S. H. (1962). Sussex. In *The Domesday Geography of South-East England.* (EDs. H. C. Darby & E. M. J. Campbell). Oxford University Press.

Knight, A. C. & Shepherd, K. B. (1985). *The Effect of Agricultural Improvement on some Upland Breeding Birds in Wales.* Newtown: Royal Society for the Protection of Birds.

Krebs, C. J. (1986). Are Lagomorphs similar to other small mammals in their population ecology? *Mammal Review* **16**: 187-194.

Kremen, C. (1992). Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**: 203-217.

Krynski, A. & Chlewski, A. (1976). The effect of the organophosphorus insecticide Sapecron on the health of the European hare. In *Ecology and Management of European Hare Populations*, 225-229 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Kutzer, E. & Frey, H. (1981). Effects of road traffic on hares. In *Proceedings of the World Lagomorph Conference*, 501-507 (Eds K. Myers and C.D. MacInnes). Ontario: University of Guelph.

Landres, P. B., Verner, J. & Thomas, J. W. (1988). Ecological uses of vertebrate indicator species: a critique. *Biological Conservation* **2**: 316-328.

Leeuwenberg, F. (1981). Game statistics in the Netherlands. In *Proceedings of the Working Group on Game Statistics.* (Eds F.

Leeuwenberg & I. Hepburn). Netherlands: International Union of Game Biologists.

Lever, C. (1977). *The Naturalized Animals of the British Isles.* London: Hutchinson.

Lincoln, G. A. (1974). Reproduction and 'March madness' in the brown hare (*Lepus europaeus*). Journal of Zoology **174**: 1-14.

Lindörf, B. (1978). Aggressive dominance rank in relation to feeding by European hare. *Viltrevy* **10**: 146-156.

Lloyd, H.G. (1968). Observations on breeding in the brown hare, *Lepus europaeus*, during the first pregnancy of the season. Journal of Zoology **156**: 521-528.

MAFF (1990). *Set-Aside.* London: Ministry of Agriculture, Fisheries and Food Publications.

MAFF (1991). *The South Downs. Environmentally Sensitive Area Report of Monitoring 1991.* London: Ministry of Agriculture, Fisheries and Food Publications.

MAFF (1992a). *Arable Area Payments: Explanatory Booklet.* London: Ministry of Agriculture, Fisheries and Food.

MAFF (1992b). *Provisional Results of June 1992 Agricultural and Horticultural Census (United Kingdom and England).* Guildford: Ministry of Agriculture, Fisheries and Food.

MAFF (1993). *CAP Reform: Arable Area Payments 1993/94. Explanatory Guide (Parts I & II).* London: Ministry of Agriculture, Fisheries and Food.

MAFF (1994). *Environmentally Sensitive Areas: The South Downs.* London: Ministry of Agriculture, Fisheries and Food.

Mankowska, E. (1976). Insecticides and the European hare reproduction. In *Ecology and Management of European Hare Populations*, 219-223 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Marchant, J. H (1983). *BTO Common Bird Census Instructions.* Tring, British Trust Ornithology.

Marchant, J. H., Hudson, R., Carter, S. P. & Whittington, P. (1990). *Population Trends in British Breeding Birds.* Tring: British Trust Ornithology.

Margules, C. & Usher, M. B. (1981). Criteria used in assessing wildlife conservation potential: a review. *Biological Conservation* **21**: 79-109.

Martinet, L. (1976). Seasonal reproduction cycles in the European hare, *Lepus europaeus*, raised in captivity: role of photoperiodicity. In *Ecology and Management of European Hare Populations*, 55-57 (Eds Z. Pielowski and Z.Pucek). Warsaw Polish Hunting Association.

Mellanby, K. (1981). *Farming and Wildlife.* London: Collins.

Middleton, A.D. (1934). Periodic fluctuations in British game populations. *Journal of Animal Ecology* 3: 231-249.

Moller, A. P. (1989). Nest site selection across field-woodland ecotones: the effect of nest predation. *Oikos* **56**: 240-246.

Monaghan, P, & Metcalfe, N.B. (1985). Group foraging in wild brown hares: effects of resource distribution and social status. *Animal Behaviour* 33: 993-999.

Morrison, M. L. (1986). Bird populations as indicators of environmental change. *Current Ornithology* 3: 429-451.

NCC (1986). *Reports on the Sites of Special Scientific Interest on the South Downs.* Lewes, Sussex: English Nature.

NCC (1989). *Guidelines for Selection of Biological SSSIs.* Peterborough: Nature Conservancy Council

Norton-Griffiths, M. (1973). Counting the Serengeti migratory wildebeest using two-stage sampling. *East African Wildlife Journal* 11: 135-149.

Noss, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4: 355-364.

O'Connor, R. J. & Shrubb, M. (1986). *Farming and Birds.* Cambridge: University Press.

Odum, E. P. (1971). *Fundamentals of Ecology.* Saunders, Pennsylvania.

Page, M. (1982). *Survey of Chalk Grassland of the South Downs, West Sussex.* Lewes, Sussex; English Nature.

Passmore, C. W. (1992). Farming in an Environmentally Sensitive Area. *Journal of the Royal Agricultural Society of England* **153**: 45-53.

Paulussen, W. (1993). *De Broudvogels van de Turnhoutse Kempen.* Brighton: Oriel Stringer.

Pehrson, A. (1983). Caecotrophy in caged mountain hares (*Lepus timidus*). *Journal of Zoology* **199**: 563-574.

Pépin, D. (1987). Dynamics of a heavily exploited population of brown hare in a large-scale farming area. *Journal of Applied Ecology* **24**: 725-734.

Pépin, D. (1989). Variation in survival of brown hare (*Lepus europaeus*) leverets from different farmland areas in the Paris basin. *Journal of Applied Ecology* **26**: 13-23.

Peterken, G. F. (1974). A method for assessing woodland flora for conservation using indicator species. *Biological Conservation* **6**: 239-245.

Petrov, P. (1976). Uber den hasen bertand in Bulgarien. In *Ecology and Management of European Hare Populations*, 1-4 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Pielowski, Z. (1969). Belt assessment as a reliable method of determining the numbers of hares. *Acta Theriologica* **14**: 133-140.

Pielowski, Z. (1971). Length of life of the hare. *Acta Theriologica* **16**: 89-94.

Pielowski, Z. (1976a). On the present state and perspectives of the European hare breeding in Poland. In *Ecology and Management of European Hare Populations*, 25-27 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Pielowski, Z. (1976b). Number of young born and dynamics of the European hare population. In *Ecology and Management of European Hare Populations*, 75-78 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Pielowski, Z. (1976c). Hunting activity vs population dynamics of the European hare. In *Ecology and Management of European Hare Populations*, 259-263 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Pielowski, Z. (1976d). The role of foxes in the reduction of the European hare population. In *Ecology and Management of European Hare Populations*, 135-148 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Pielowski, Z. (1981). Yearly balance of European hare population. In *Proceedings of the World Lagomorph Conference*, 536-540 (Eds K. Myers & C.D. MacInnes). Ontario: University of Guelph.

Pielowski, Z. & Pucek, Z. (Eds) (1976). *The Ecology and Management of European Hare Populations*: Proceedings of an International Symposium Held in Poznan on December 23-24, 1974. Warsaw: The Polish Hunting Association.

Pielowski, Z. and Raczynski, J. (1976). Ecological conditions and rational management of hare Populations. In *Ecology and Management of European Hare Populations*, 269-286 (Eds Z. Pielowski and Z.Pucek). Warsaw, Polish Hunting Association.

Poole, R. W. (1974). *An Introduction to Quantitative Ecology*. Tokyo: McGraw-Hill.

Potts G.R & Vickerman G. P. (1974). Studies on the cereal ecosystem. *Advances in Ecological Research* **8**: 107-197.

Potts, G. R. (1980). The effects of modern agriculture, nest predation, and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Advances in Ecological Research* **11**: 1-79.

Potts, G. R. (1992). The research department. *The Game Conservancy Review of 1991*, 23-27. Fordingbridge: The Game Conservancy Trust.

Poulsen, J. G. & Sotherton, N. (1993). Skylarks on farmland: a species in decline. In *The Game Conservancy Review of 1992*, 58-60. Fordingbridge: The Game Conservancy Trust.

Raczynski, J. (1964). Studies on the European hare V: Reproduction. *Acta Theriologica* **9**: 305-352.

Rajska, E. (1968). Estimation of European hare population density depending on the width of the assessment belt. *Acta Theriologica* **13**: 35-53.

Ratcliffe, D.A. (1980). *The Peregrine Falcon*. Calton: Poyser.

Reynolds, J. & Tapper, S.C. (1989). Foxes and hares. *The Game Conservancy Annual Review of 1988*, 98-101. Fordingbridge: The Game Conservancy Trust.

Robbins, C. S. (1981). Effect of time of day on bird activity. *Studies in Avian Biology* **6**: 275-286.

Robson, R. W. & Williamson, K. (1972). The breeding birds of a Westmorland farm. *Bird Study* **19**: 202-214.

Rollin, N. (1931). The varying length of lark song. *The Scottish Naturalist* 47-54.

Salzmann-Wendeler, I. (1976) Feldhasen-abschusazahlen in der Schweiz. In *Ecology and Management of European Hare Populations*, 35-40 (Eds Z. Pielowski and Z.Pucek). Warsaw: Polish Hunting Association.

Sawyer, F. E. (1792). *Map showing Brighton and the Laines in 1792*. (Copy held in Brighton Public Library.)

Schlapfer, A. (1988). [Population ecology of the skylark *Alauda arvensis* in intensively used farmland.] *Der Ornithologische Beobachter* 85: 309-371.

Schneider, E. (1981). Studies on the social behaviour of the brown hare. In *Proceedings of the World Lagomorph Conference*, 340-348 (Eds K. Myers & C. D. MacInnes). Ontario: University of Guelph.

Shrubb, M. (1979). *The Birds of Sussex. Their Present Status*. Chichester: Phillimore.

Smith, J. N. M., Krebs, C. J., Sinclair, A. R. E. & Boonstra, R. (1988). Population biology of snowshoe hares II: Interactions with winter food plants. *Journal of Animal Ecology* 57: 269-286.

Sotherton, N. (1992). The environmental benefits of conservation headlands in cereal fields. *Outlook on Agriculture* 21: 219-224.

Soule, D. F. & Keppel, G. S. (1988). *Marine Organisms as Indicators.* New York: Springer-Verlag.

Soule, D. F. (1988). Marine organisms as indicators: reality or wishful thinking? In *Marine Organisms as Indicators*, 1-11 (Eds D. F. Soule & G. S. Keppel). New York: Springer Verlag.

Standgaard, H. & Asfeg, T. (1980). The Danish Bag Record II. *Danish Review of Game Biology* **11**: 312.

Stoate, C, & Szczur, J. (1993). The birds of Loddington. *The Game Conservancy Review of 1992*, 42-47. Fordingbridge: The Game Conservancy Trust.

Stoate, C. & Tapper, S.C (1990). The hare conservation project. *The Game Conservancy Review of 1989:* 50-53. Fordingbridge: The Game Conservancy Trust.

Stoate, C. & Tapper, S. C (1989). Coursing and shooting: their effect on hare numbers. *The Game Conservancy Annual 1988*: 95-97. Fordingbridge: The Game Conservancy Trust.

Suzuki, S., Tanioka, K., Uchimura, S. & Marumoto, T. (1952). [The hovering height of skylarks.] *J. Agr. Met. Japan* **7**: 71-73.

Tapper, S. C. (1976). Hares on the West Sussex Downs. *The Game Conservancy Review of 1975*: 37-44. Fordingbridge: The Game Conservancy Trust.

Tapper, S. C. (1987). Cycles in game-bag records of hares and rabbits in Britain. *Symposium of the Zoological Society of London* **58**: 79-98.

Tapper, S. C. (1989). The increase in oilseed rape production and its effects on vertebrate herbivores. *Aspects of Applied Biology* **23**: 365-370.

Tapper, S. C. (1991). *Brown hare.* In *The Handbook of British Mammals* (Eds G. B. Corbet & S. Harris). Oxford: Blackwell Scientific Publications.

Tapper, S. C. & Barnes, R. F. W. (1986). Influence of farming practice on the ecology of the brown hare (*Lepus europaeus*). *Journal of Applied Ecology* **23**: 39-52.

Tapper, S. C., Brockless, M. & Potts, D. (1991). The Salisbury Plain predation experiment: the conclusion. *The Game Conservancy Review of 1990*: 87-91.

Tapper, S. & Parsons, N. (1984). The changing status of the brown hare (*Lepus capensis* L.) in Britain. *Mammal Review* **14**: 57-70.

Thomas, A. S. (1963). Further changes in vegetation since the advent of myxomatosis. *Journal of Ecology* **51**:151-186.

Tittensor, R. M. (1979). The evolution of the landscape in the Chilgrove area. In *Chichester Excavations, 4. The Roman Villas at Chilgrove and Upmarden* (Ed. A. Down). Chichester: Phillimore.

Tittensor, R. M. (1980). Ecological history of Yew *Taxus baccata* L. in Southern England. *Biological Conservation* **17**: 243-265.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**: 893-901.

Walford-Lloyd, E. (1924). *Southdown sheep*. T. G. Willis & Co.

Walpole-Bond, J. (1938). *A History of the Birds of Sussex*. London: Witherby.

Whitbread, T (1993). *A Vision for the South Downs*. Henfield: Sussex Wildlife Trust.

Wilkinson, L. (1990). *Systat: The System for Statistics*. Systat, Evanston, illinois, USA.

Wilhm, J. H. (1975). Biological indicators of pollution. In *River Ecology* (Ed. B. A. Whitton). London: Blackwell.

Williamson, K. (1967). The bird community of farmland. *Bird Study* **14**: 210-226.

Wilson, P. & Sotherton, N. (1994). *Field Guide to rare arable flowers*. Game Conservany, Fordingbridge.

Witherby, H. F., Jourdain, F. C . R., Ticehurst, N. F. and Tucker, B. W. (1938). *The Handbook of British Birds.* London: Witherby.

Zar, J. H. (1984). *Biostatistical analysis.* New York, Prentice-Hall.

Appendices

List of contents

Appendix A List of the species discussed in Chapter 2

Brown hare	*Lepus europaeus*
Wood mouse	*Apodemus sylvaticus*
Hedgehog	*Erinaceus europaeus*
Common shrew	*Sorex aranaeus*
Badger	*Meles meles*
Mole	*Talpa europaea*
Rabbit	*Oryctolagus cuniculus*
Pygmy shrew	*Sorex minutus*
House mouse	*Mus musculus*
Field vole	Microtus agrestis
Harvest mouse	*Micromys minutus*
Bank vole	*Clethrionomys glareolus*
Fox	*Vulpes vulpes*
Dormouse	*Muscardinus avellanarius*
Squirrel	*Sciurus carolinensis*
Roe deer	*Capreolus capreolus*
Weasel	*Mustela nivalis*
Stoat	*Mustela erminea*
Skylark	*Alauda arvensis*
Lapwing	*Vanellus vanellus*
French partridge	*Alectoris rufa*
Grey partridge	*Perdix perdix*
Meadow pipit	*Anthus pratensis*

Appendix B The farmer questionnaire

As you know I'm trying to estimate the size of the populations of brown hares and skylarks on the Downs between Lewes and Worthing. I'm also interested in the way farm management practices affect these species.

This questionnaire has six parts and should not take long to complete.

All information is confidential.

Part 1: Hares and Larks

a) Do you see hares on the farm regularly?

b) Roughly how many do you see on your farm?

c) Please indicate on the map where you see them.

d) Which crops do you see them in?

crop type	day/night	time of year (eg season)
winter cereals		
spring cereals		
stubble		
*ley grass		
*permanent pasture		
*ESA grass		
set-aside		
oilseed rape		
linseed		
beans		
other		

*stocked & unstocked

e) Have hare numbers changed on this farm in the last five years?

f) Over the last 20 years? (if applicable)

g) Do you have any opinions as to why this may be?

h) Have you found any dead hares?

Where?

At which time of year?

Do you know or can you suggest why they died?

i) Do you see larks on the farm regularly?

j) Roughly how many on your farm?

k) Please indicate on the map where you see them.

l) Which crops do you see them in?

crop type	day/night	time of year (eg season)
winter cereals		
spring cereals		
stubble		
*ley grass		
*permanent pasture		
*ESA grass		
set-aside		
oilseed rape		
linseed		
beans		
other		

*stocked & unstocked

m) Have lark numbers changed on this farm in the last five years?

f) Over the last 20 years? (if applicable)

g) Do you have any opinions as to why this may be?

h) Have you found any dead larks or damaged nests?

Where?

When?

Do you know or can you suggest why they died?

Part 2: Predator control.

I'm interested in what effects predator control may have on these species.

a) Do you run a shoot?

b) Employ a keeper?

c) Allow others to shoot on your farm?

d) Shoot to control pests?

e) Which species do you control as pests?

	time of year	methods	no.killed
foxes			
rabbits			
hares			
crows			
magpies			
pigeons			
others			

f) Have you noticed any dramatic changes in the numbers of any of these species on the farm in the last five years ?

Over the last 20 years? (if applicable)

g) Do you have trouble with hare poachers?

please could you elaborate?

h) Do you allow the foxhounds over your land?

i) Do you allow the beagles over your land?

Part 3: Arable crop management.

a) Please outline your general crop rotation.

b) How has this changed in the last five years?

c) Why have you made these changes?

d) Which chemicals do you apply to your winter wheat?

Type	no.applications	rate
herbicides		
fungicides		
insecticides		
fertiliser		
growth regulators		

Part 4: Grassland management:

a) Please indicate on the map where you have:

i) ESA grassland:

existing downland grass

arable reversion grass (rye-grass or traditional species?)

ii) Permanent pasture (not ESA)

iii) Short-term ley grass

iv) Other

b) Do you intend to increase or decrease ESA grassland area?

c) How often do you cut silage?

dates?

d) Do you make hay?

cutting date?

e) What chemicals do you apply to your grassland?

Fertiliser: nos of applications? rate?

Herbicides: nos of applications? rate?

f) Stocking:

What types of grazing stock do you keep?

Type	Number	period of year at grass
Sheep		
Beef		
Dairy cows		
Horses		
Others		

g) Has your overall stocking rate (per forage hectare) changed with the introduction of ESA ? In what ways?

h) Have you cleared scrub?

i) Removed/planted trees or hedges ?

j) Do you have conservation headlands?

Part 5: Rotational set-aside management.

a) How did/are you managing your rotational set-aside ?

1992/93 1993/94

Regenerated stubble ?

Planted cover crop ?

type?

b) Do you intend to cultivate the set-aside to control weeds?

when ?

c) Do you intend to top the set-aside?

when ?

d) Do you have a reason for the timing of these operations?

e) Do you have other set-aside schemes?

Part 6: Wildlife and conservation in general

a) What interesting wildlife do you have on the farm?

b) Do you take any measures to conserve these species?

what?

c) Which of these interesting species have you seen on

the rotational set-aside?

ESA grassland

other crops ?

d) Have you asked for/received conservation advice on the farm?

From who?

What did it concern? (game management, tree planting, ponds, whole farm plan?)

e) Did you burn straw?

f) What are you doing as an alternative?

Appendix C1

Table C1 Relative fox control effort, approximate number of hares shot over study period and presence or absence of rabbit control, beagling and reported hare poaching during study period on study farms.

Farm	Foxes	Hares	Rabbits	Beagling	Poaching
A	75	< 5	yes	yes	yes
B	37	no	yes	yes	yes
C	0	no	yes	no	no
D	No report	no	yes	yes	no
E	60	no	yes	yes	yes
F	0	no	yes	yes	yes
G	0	no	yes	yes	no
H	75	< 5	yes	yes	yes
I	0	no	yes	no	no
J	100	10+	yes	yes	yes
K	100	10+	yes	yes	yes
L	40	no	yes	yes	no
M	100	143+	yes	yes	yes
N	100	20+	yes	yes	no
O	0	0	yes	no	no
P	3	0	yes	yes	no
Q	0	0	yes	no	yes

Appendix C2 Negative binomial distribution

Table C2a Expected and observed distribution of hares among 121 spotlight samples made on 10 farms in winter 1991/92. The expected values were estimated using the negative binomial distribution function, and an estimate of *k* (a parameter of the distribution) based on the iterative equation:

$$k\log(1+\text{mean hares per sample}/k) = \log(N/y)$$

where N is the number of spotlight samples and y is the number of samples with no hares (Poole, 1974). *k* was estimated as 0.367.

	No. samples:		
No. hares/sample	observed	expected	X^2
0	90	90	0.00
1	15	18.3	0.60
2	11	6.9	2.44
>3	5	5.7	0.09
Totals	121	120.9	3.13 (1df) NS

Table C2b The data used to produce Table A2a.

	No. samples/farm									
No. hares/sample	A	D	E	G	H	I	J	K	L	P
0	11	13	8	9	4	6	7	11	12	9
1	1	1	2	2	1	1	2	0	1	4
2	0	3	1	0	0	0	4	1	1	1
3	0	0	1	1	0	0	1	0	0	0
4	0	1	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	1	0	0	0

Appendix D Brown hare data

KEY

SA, spring arable; WA, winter arable; WC, winter cereal; GR, grass; GR(S), stocked grassland; GR(noS), unstocked grassland; DT, downland turf (unimproved chalk grassland); SB, scrub; WD, woodland; P, plough; St, stubbles; CC, catch crops (eg stubble turnips, kale etc); SE, seed-bed; SS, set-aside.

Table D1 The number of hares seen flushed by the Brighton & Storrington Foot Beagles (BSFB) on farms where they hunted in the winters of 1991/1992, 1992/1993 & 1993/1994; and an estimate of rabbit density (rabbits/km2) on the study farms in the winter of 1991/1992, calculated from data collected during hare spotlight counts.

* = no data available.

Farm	Hares flushed by BSFB			Rabbit density
	91/92	92/93	93/94	91/92
A	1	*	1	35
B	0	0	0	231
C	*	*	*	6
D	4	3	5	16.5
E	5	6	6	30
F	0	*	*	*
G	3	*	*	21
H	1	*	1	34
I	1	*	*	*
J	6	3	6	40.5
K	*	*	*	40.5
L	4	3	1	2.5
M	20	1	*	3
N	*	3	8	3
O	*	1	*	3
P	1	6	8	*
Q	*	*	*	*

Table D2ai The area (ha) in each habitat type, total area (ha) and habitat diversity of each farm in winter 1991/1992. H, Shannon-Weiner diversity measure; J, Shannon-Weiner measure of evenness (relative diversity) (Zar, 1984).

Farm	St	WC	BC	DT	GR*	SB	WD	P	Total	H	J
A	35	35	0	15	80	0	15	44	224	0.708	0.784
B	20	0	0	41	120	47	25	0	253	0.604	0.669
C	0	162	0	7	25	20	0	0	214	0.345	0.382
D	57	146	5	15	187	80	7	10	507	0.673	0.745
E	71	80	32	28	6	0	12	0	229	0.657	0.727
F	0	145	0	0	82	0	65	40	332	0.557	0.616
G	49	57	0	29	13	4	2	5	159	0.652	0.722
H	0	67	3	30	15	5	5	21	146	0.654	0.724
I	0	62	5	20	26	2	17	0	132	0.613	0.679
J	7	0	0	41	384	17	1	0	450	0.241	0.267
K	0	179	1	8	70	8	6	0	272	0.407	0.451
L	161	202	32	27	21	2	0	0	445	0.545	0.603
M	0	444	0	8	11	5	0	0	468	0.111	0.123
N	47	33	20	45	244	25	44	108	566	0.741	0.821
O	0	0	0	36	332	0	0	0	368	0.139	0.154
P	32	110	10	31	89	8	0	0	280	0.627	0.694
Q	24	54	5	30	115	1	0	65	294	0.668	0.740

*Total area of non-ESA grass = 394ha (21% of the total area of grassland). This was usually associated with dairy farms.

Table D2aii The area (ha) in each habitat type, total area (ha) and habitat diversity of each farm in summer 1992. H, Shannon-Weiner diversity measure (Zar, 1984).

Farm	SA	WA	DT	GR	SB	WD	Total	H
A	79	35	15	80	0	15	224	0.776
B	35	0	41	105	47	25	253	0.824
C	0	162	7	0	0	45	214	0.364
D	38	167	15	200	80	7	507	0.771
E	77	112	28	0	0	12	229	0.630
F	45	122	0	92	0	73	332	0.742
G	52	55	38	8	4	2	159	0.767
H	21	70	30	15	5	5	146	0.793
I	0	67	20	26	2	17	132	0.713
J	7	0	41	384	17	1	450	0.310
K	54	129	7	68	7	7	272	0.729
L	161	234	27	21	2	0	445	0.584
M	0	442	7	14	5	0	468	0.150
N	166	33	45	252	26	44	566	0.797
O	0	0	36	332	0	0	368	0.179
P	32	120	31	89	8	0	280	0.738

Table D2b Total numbers of hares seen on each farm, and the total area (ha) sampled on each farm by spotlight in winter 1991/1992.

Farm	No. hares	Sample area
A	1	59.5
B	0	42.0
C	0	63.0
D	11	79.0
E	7	63.5
F	0	51.0
G	5	76.0
H	1	29.5
I	1	28.5
J	18	70.0
K	2	51.0
L	3	80.0
M	12	37.5
N	16	93.0
O	0	71.0
P	6	48.0
Q	21	250.0

Table D2c The area (ha) in each habitat type, total area (ha) and habitat diversity of each farm in winter 1992/1993. H, Shannon-Weiner diversity measure; J, Shannon-Weiner measure of evenness (relative diversity) (Zar, 1984).
(NB J and H have the same value as there are 10 habitat classes).

F	St*	WC	BC	DT	GR	SB	WD	P	SE	CC	Total	H
A	0	51	0	15	29	0	15	85	0	29	224	0.694
B	16	20	0	45	92	43	25	12	0	0	253	0.749
C	162	0	0	7	25	20	0	0	0	0	214	0.346
D	60	69	0	15	207	80	7	33	10	26	507	0.761
E	12	152	15	28	0	0	12	10	0	0	229	0.501
F	38	97	0	0	93	0	65	13	26	0	332	0.699
G	30	58	0	29	19	4	2	17	0	0	159	0.709
H	42	21	0	30	15	5	5	18	10	0	146	0.824
I	24	32	0	20	32	2	17	0	5	0	132	0.753
J	7	0	0	41	370	17	1	0	0	14	450	0.300
K	30	132	0	8	70	8	6	7	0	11	272	0.633
L	0	0	0	27	364	2	1	0	0	0	394	0.130
M	60	374	0	8	11	5	0	0	0	10	468	0.317
N	103	52	0	45	225	25	44	0	56	16	566	0.766
O	0	0	0	36	332	0	0	0	0	0	368	0.139
P	22	119	0	31	80	8	0	20	0	0	280	0.633
Q	20	32	0	30	151	1	0	48	0	12	294	0.627

*10 study farms had rotational set-aside in the study area, 3 farmers topped their set-aside I(20ha), M(20ha), N(34ha); 7 farmers cultivated their set-aside C(162ha), D(9ha), G(15ha), H(42ha), K(10ha), P(30ha), Q(20ha).

Table D2d The numbers of hares and the habitat types in which they were present during the first spotlight count of winter 1992/1993 (October). In this table 0 can indicate (1) that there were no hares present in a habitat type, (2) that a habitat type was not represented on a particular farm or (3) that a habitat type was not lamped. Reference to Table D2c and Table D2e indicates which is the case.

Farm	ST	WC	DT	GR(S)	GR(noS)	TOTAL
A	0	0	0	0	0	0
B	0	0	0	0	0	0
C	0	0	0	0	0	0
D	3	0	0	0	2	5
E	0	0	0	0	0	0
F			Not counted			
G	0	0	0	0	0	0
H	0	0	0	0	0	0
I	0	0	0	0	0	0
J	3	0	4	1	2	10
K	3	2	0	0	0	5
L	0	0	0	0	0	0
M	15	0	0	0	0	15
N	20	7	9	0	38	74
O	0	0	0	0	0	0
P	2	5	0	0	0	7
Q	5	0	0	0	4	9

Table D2e The areas (ha) of crop types covered by spotlight, in the first count of hares in winter 1992/1993 (October).

Farm	ST	WC	DT	GR(S)	GR(noS)	P	CC	SE
A	11.0	0.0	5.5	2.0	31.5	0.0	16.5	19.5
B	6.5	0.0	2.5	0.0	33.0	0.0	0.0	0.0
C	61.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
D	36.5	0.0	0.0	15.0	10.0	0.0	0.0	15.5
E	4.0	20.0	0.0	0.0	0.0	1.5	0.0	64.0
F			Not counted					
G	49.0	0.0	0.0	0.0	21.5	9.5	0.0	0.0
H	32.0	0.0	0.0	8.5	0.0	12.5	0.0	11.0
I	16.5	0.0	0.0	0.0	3.5	0.0	0.0	10.0
J	4.5	0.0	15.0	10.0	17.0	0.0	5.5	0.0
K	13.5	6.0	0.0	0.0	2.5	4.5	5.5	4.5
L	0.0	0.0	0.0	50.0	56.0	0.0	0.0	0.0
M	45.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N	60.0	10.0	10.0	0.0	20.0	2.5	2.5	12.5
O	0.0	0.0	0.0	57.0	50.0	0.0	0.0	0.0
P	16.0	14.5	2.0	0.0	24.0	1.0	0.0	11.5
Q	15.5	3.5	5.0	20.0	36.0	13.0	0.0	0.0

Table D2f The numbers of hares and the habitat types in which they were present during the second spotlight count of winter 1992/1993 (December/January). In this table 0 can indicate (1) that there were no hares present in a habitat type, (2) that a habitat type was not represented on a particular farm or (3) that a habitat type was not lamped. Reference to Table D2c and Table D2g indicates which is the case.

Farm	ST	WC	DT	GR(S)	GR(noS)	TOTAL
A	0	0	0	0	1	1
B	0	0	0	0	0	0
C	0	0	0	0	0	0
D	0	3	0	0	2	5
E	1	2	0	0	0	3
F	0	0	0	0	0	0
G	2	3	0	0	0	5
H	0	0	0	1	0	1
I	0	0	0	0	5	5
J	0	0	0	3	7	10
K	0	13	0	0	2	15
L	0	0	0	0	0	0
M			Not counted			
N	7	6	0	0	6	19
O	0	0	0	0	0	0
P	0	8	0	0	3	11
Q	0	15	0	0	11	26

Table D2g The areas (ha) of crop types covered by spotlight, in the second count of hares in winter 1992/1993 (December/January).

Farm	ST	WC	DT	GR(S)	GR(noS)	P	CC	SE
A	0.0	25.5	2.0	0.0	19.0	8.5	5.5	0.0
B	6.5	3.5	2.5	4.5	28.5	0.0	0.0	0.0
C	51.0	0.0	0.0	0.0	8.5	0.0	0.0	0.0
D	3.0	13.5	0.0	0.0	34.0	0.0	0.0	4.5
E	4.0	99.0	0.0	0.0	0.0	1.5	0.0	0.0
F	0.0	18.5	0.0	16.5	20.5	6.0	0.0	18.0
G	21.0	17.0	0.0	0.0	7.0	3.5	0.0	0.0
H	12.0	6.5	0.0	6.0	4.0	0.0	0.0	4.0
I	9.5	12.5	0.0	0.0	10.0	0.0	0.0	3.0
J	4.5	0.0	9.5	10.0	16.0	0.0	1.0	0.0
K	18.5	14.0	0.0	0.0	2.5	2.5	6.5	0.0
L	24.0	0.0	0.0	13.5	85.5	0.0	0.0	0.0
M			Not counted					
N	57.5	34.5	10.0	6.0	43.5	0.0	0.0	0.0
O	0.0	0.0	0.0	58.5	50.0	0.0	0.0	0.0
P	3.5	45.0	2.0	5.0	17.0	4.0	0.0	0.0
Q	2.5	13.5	3.0	21.0	41.5	17.0	5.5	0.0

Table D2h The numbers of hares and the habitat types in which they were present during the third spotlight count of winter 1992/1993 (February/March). In this table 0 can indicate (1) that there were no hares present in a habitat type, (2) that a habitat type was not represented on a particular farm or (3) that a habitat type was not lamped. Reference to Table D2c and Table D2i indicates which is the case.

Farm	ST	WC	DT	GR(S)	GR(noS)	TOTAL
A	0	0	0	0	0	0
B	0	0	0	0	0	0
C	0	0	0	0	0	0
D	0	5	0	0	2	7
E	0	5	0	0	0	5
F	0	0	0	0	0	0
G	0	2	0	0	1	3
H	1	0	0	0	0	1
I	0	0	0	0	2	2
J	3	0	1	7	1	12
K	1	1	0	0	0	2
L	0	0	0	0	0	0
M	1	0	0	0	0	1
N	3	7	1	0	5	16
O	0	0	0	0	0	0
P	1	8	0	0	2	11
Q	0	15	0	0	0	15

Table D2i The areas (ha) of crop types covered by spotlight, in the third count of hares in winter 1992/1993 (February/March).

Farm	ST	WC	DT	GR(S)	GR(noS)	P	CC	SE
A	0.0	27.5	3.0	0.0	20.5	15.0	0.0	0.0
B	0.0	3.5	2.5	10.0	20.5	0.0	0.0	6.5
C	56.0	0.0	0.0	0.0	7.5	0.0	0.0	0.0
D	0.0	16.5	0.0	3.0	24.0	3.0	1.5	0.0
E	0.0	77.5	2.0	0.0	0.0	5.0	0.0	0.0
F	0.0	42.5	0.0	17.0	21.0	0.0	0.0	0.0
G	17.5	21.0	5.0	0.0	5.0	9.0	0.0	0.0
H	16.0	13.0	3.0	14.0	0.0	9.0	0.0	0.0
I	6.5	14.5	0.0	0.0	11.0	2.0	0.0	1.5
J	7.0	0.0	20.0	36.0	30.0	0.0	0.0	0.0
K	4.0	16.0	1.0	0.0	0.0	3.0	9.0	10.0
L	0.0	0.0	0.0	74.0	49.0	0.0	0.0	0.0
M	15.0	37.0	0.0	0.0	0.0	0.0	0.0	0.0
N	10.0	51.0	10.0	0.0	35.0	10.0	0.0	0.0
O	0.0	0.0	0.0	72.0	50.0	0.0	0.0	0.0
P	6.0	66.5	0.0	6.0	23.0	2.5	0.0	0.0
Q	6.5	17.5	0.0	6.0	22.5	16.5	3.5	0.0

Table D3a The area (ha) in each habitat type, total area (ha) and habitat diversity of each farm in winter 1993/1994. H, Shannon-Weiner diversity measure; J, Shannon-Weiner measure of evenness (relative diversity) (Zar, 1984).
(NB J and H have the same value as there are 10 habitat classes).

F	St	WC	BC	DT	GR	SB	WD	P	SE	CC	Total	H
A	49	43	0	15	29	0	15	29	0	44	224	0.80
B	16	20	0	45	104	43	25	0	0	0	253	0.69
C	0	162	0	7	25	20	0	0	0	0	214	0.35
D	30	120	0	15	207	80	7	20	10	18	507	0.72
E	99	32	26	28	0	0	12	25	0	7	229	0.71
F	38	97	0	0	93	0	65	0	26	13	332	0.69
G	40	60	0	29	19	4	2	5	0	0	159	0.67
H	31	67	0	30	5	5	5	0	10	3	146	0.63
I	14	25	22	20	32	2	17	0	5	0	132	0.79
J	0	0	0	41	370	17	1	7	0	14	450	0.30
K	44	34	0	8	68	8	6	104	0	0	272	0.68
L	0	0	0	27	364	2	1	0	0	0	394	0.13
M	60	374	0	8	11	5	0	0	0	10	468	0.32
N	103	52	0	45	225	25	44	0	56	16	566	0.77
O	0	0	0	36	332	0	0	0	0	0	368	0.14
P	59	60	0	31	87	8	0	35	0	0	280	0.71
Q	13	51	0	30	149	1	0	30	0	15	294	0.65

Table D3b The numbers of hares, and the habitat types in which they were present during the single spotlight count of winter 1993/1994.

Farm	ST	WC	DT	GR(S)	GR(noS)	TOTAL HARES	TOTAL (ha)
A	0	0	0	0	0	0	66.5
B	0	0	0	0	0	0	40.0
C	0	0	0	0	0	0	52.5
D	1	0	0	0	17	18	120.0
E	2	5	0	0	0	7	100.0
F	0	0	0	0	0	0	52.0
G	0	2	0	0	0	2	64.0
H	0	0	0	0	0	0	27.5
I	0	0	0	0	2	2	31.0
J	0	0	2	0	18	20	93.0
K	2	7	0	0	0	9	43.0
L	0	0	0	0	0	0	76.0
M	0	1	0	0	0	1	52.0
N	8	9	0	0	3	20	175.0
O	0	0	0	3	0	3	111.0
P	0	4	0	0	6	10	130.0
Q	0	1	0	4	13	18	111.0

Appendix E Skylark data

KEY

SA, spring arable; WA, winter arable; WC, winter cereal; GR, grass; GR(S), stocked grassland; GR(noS), unstocked grassland; DT, downland turf (unimproved chalk grassland); SB, scrub; WD, woodland; P, plough; St, stubbles; CC, catch crops (eg stubble turnips, kale etc); SE, seed-bed; SS, set-aside.

Table E1a Length of habitats represented in transects, 1992 breeding season. (These measurements are in cm, as measured from a map. To calculate the actual Length of the transect multiply each cm by 90m. To calculate the area in which skylarks could be detected, then multiply by 200m).

Farm	SA	WA	DT	GR	SB	WD	TOTAL
A	21.0	11.0	4.5	20.0	0.0	1.5	58.0
B	6.5	0.0	9.5	33.0	10.5	5.0	64.5
C	0.0	44.0	0.0	0.0	16.0	0.0	60.0
D	0.0	14.0	5.0	31.0	7.0	1.0	58.0
E	29.5	35.0	7.0	0.0	0.0	12.5	84.0
F	13.5	24.5	0.0	13.0	0.0	10.5	61.5
G	14.0	12.0	13.0	0.0	2.0	0.0	41.0
H	13.0	23.5	13.5	6.0	1.5	1.0	58.5
I	0.0	25.5	5.0	10.0	3.0	7.5	51.0
J	3.5	0.0	1.0	51.5	3.0	0.5	59.5
K	23.0	32.0	2.0	9.0	2.0	0.0	68.0
L	34.0	54.0	0.0	3.5	0.0	0.0	91.5
M	0.0	117.0	0.5	1.0	1.0	0.0	119.5
N	56.0	6.5	0.0	26.5	1.0	3.5	93.5
O	0.0	0.0	7.5	68.5	0.0	0.0	76.0
P	5.5	40.5	1.5	19.5	2.0	0.0	69.0

Table E1b Numbers of singing male skylarks in the habitats along the 16 transects walked in the first brood period of 1992 breeding season

Farm	SA	WA	DT	GR	SB	WD	TOTAL
A	1	3	0	2	0	0	6
B	0	0	0	6	0	0	6
C	0	6	0	0	0	0	6
D	0	3	0	3	0	0	6
E	2	7	0	0	0	0	9
F	1	4	0	1	0	0	6
G	2	1	0	0	0	0	3
H	0	5	0	1	0	0	6
I	0	1	0	0	0	0	1
J	0	0	0	5	0	0	5
K	4	4	0	0	0	0	8
L	2	18	0	0	0	0	20
M	0	9	0	0	0	0	9
N	2	0	0	3	0	0	5
O	0	0	0	7	0	0	7
P	0	3	0	1	0	0	4

Table E1c Numbers of singing male skylarks in the habitats along the 12 transects walked in the second brood period of 1992 breeding season.

Farm	SA	WA	DT	GR	SB	WD	TOTAL
A	3	0	0	0	0	0	3
B	3	0	0	3	0	0	6
C	0	1	0	0	0	0	1
D	0	3	1	3	0	0	7
E	5	4	1	0	0	0	10
F	2	0	0	0	0	0	2
H	0	4	4	0	0	0	8
I	0	1	0	0	0	0	1
J	0	0	0	5	0	0	5
L	3	9	0	1	0	0	13
O	0	0	0	11	0	0	11
P	0	1	0	1	0	0	2

Table E2a Length of habitats represented in transects, 1993 breeding season. (These measurements are in cm, as measured from a map. To calculate the actual Length of the transect multiply each cm by 90m. To calculate the area in which skylarks could be detected, then multiply by 200m).

* = set-aside topped, all other set-aside cultivated after May 1.

Farm	SA	WA	DT	GR	SB	WD	SS	TOTAL
A	27.0	21.0	4.5	3.0	1.0	1.5	0.0	58.0
B	15.0	0.0	0.0	41.0	8.5	0.0	0.0	64.5
C	13.0	0.0	0.0	8.0	5.0	4.0	30.0	60.0
D	9.0	9.0	4.0	28.0	3.0	5.0	7.0	65.0
E	16.0	48.5	7.0	0.0	0.0	12.5	0.0	84.0
F	19.0	17.0	0.0	15.0	0.0	10.0	0.0	61.0
G	13.0	27.0	7.0	10.0	1.0	1.0	6.0	65.0
H	9.0	14.0	13.5	1.5	1.5	1.0	18.0	58.5
I	0.0	12.0	8.0	4.0	1.0	2.0	6.0*	33.0
J	3.5	0.0	1.0	51.5	3.0	0.5	0.0	59.5
K	12.0	36.0	2.0	4.0	2.0	2.0	1.0	59.0
L	0.0	0.0	0.0	85.0	0.0	0.0	0.0	85.0
M	0.0	82.0	0.5	1.0	1.0	0.0	35.0*	119.5
N	40.0	9.0	0.0	20.0	1.0	3.5	20.0*	93.5
O	0.0	0.0	7.5	68.5	0.0	0.0	0.0	76.0
P	6.0	27.5	1.5	26.0	2.0	0.0	6.0	69.0
Q	11.0	13.0	5.0	28.0	2.0	0.0	8.0	67.0

Table E2b Numbers of singing male skylarks in the habitats along the 17 transects walked in the first brood period of 1993 breeding season

Farm	SA	WA	SS	DT	GR	SB	WD	TOTAL
A	2	3	0	0	0	0	0	5
B	1	0	0	0	9	0	0	10
C	0	0	14	0	0	0	0	14
D	0	3	3	0	5	0	0	11
E	3	13	0	0	0	0	0	16
F	1	4	0	0	1	0	0	6
G	0	6	4	1	1	0	0	12
H	1	4	8	1	0	0	0	14
I	0	3	2	0	1	0	0	6
J	0	0	0	0	9	0	0	9
K	1	9	0	0	0	0	0	10
L	0	0	0	0	19	0	0	19
M	0	16	5	0	0	0	0	21
N	1	5	5	0	4	0	0	15
O	0	0	0	0	15	0	0	15
P	0	4	4	0	2	0	0	10
Q	3	6	5	2	11	0	0	27

Table E2c Numbers of singing male skylarks in the habitats along the 17 transects walked in the second brood period of 1992 breeding season.

Farm	SA	WA	SS	DT	GR	SB	WD	TOTAL
A	4	3	0	0	0	0	0	7
B	3	0	0	0	7	0	0	10
C	1	0	8	0	0	0	0	9
D	4	2	2	0	6	0	0	14
E	5	9	0	0	0	0	0	14
F	1	0	0	0	0	0	0	1
G	6	0	0	0	0	0	0	6
H	4	3	3	3	1	0	0	14
I	0	0	2	1	1	0	0	4
J	0	0	0	0	5	0	0	5
K	5	8	0	0	0	0	0	13
L	0	0	0	0	16	0	0	16
M	0	11	7	0	1	0	0	19
N	6	5	7	0	2	0	0	20
O	0	0	0	0	20	0	0	20
P	2	1	2	0	1	0	0	6
Q	3	3	0	3	11	0	0	20

Table E3a Number of singing male skylarks along a 1.25km transect on Offham farm. Counts were made at different times of day on different days, throughout the 1992 breeding season. The maximum number of singing males was 8.

KEY: Time = decimal hours after dawn (eg 1.50 = 1 hour 30 minutes after dawn); Wind = windspeed (L, light; VL, very light; M, moderate; S, still; SR, strong); °C = atmospheric temperature in degrees centigrade; mmHg = atmospheric pressure in millimetres of Mercury (F, falling; R, rising; S, stable); CC = cloud cover (CL, clear; O/C, over-cast; H, hazy; F, fog); Larks = the number of singing male skylarks counted each time the transect was walked.

Date	Time	Wind	°C	mmHg	CC	LARKS
4/4	4.10	L	12.0	755R	CL	7
5/4	0.96	VL	4.0	759S	CL	6
6/4	0.84	M	5.0	755F	O/C	3
7/4	0.88	L	7.0	745S	O/C	6
8/4	0.91	L	6.0	752R	H	4
11/4	1.11	S	8.5	764F	H	8
12/4	0.64	L	11	760S	O/C	6
13/4	7.60	SR	10.5	760S	CL	6
14/4	8.63	SR	6.0	755F	O/C	0
15/4	6.92	M	9.0	748R	O/C	6
16/4	3.28	M	6.0	765R	CL	7
17/4	4.83	S	12.0	768S	F	7
21/4	7.92	S	19.0	760S	CL	5
2/5	4.42	M	10.0	760R	CL	7
13/5	12.47	L	18.0	767F	CL	6
16/5	12.05	M	18.0	776F	CL	3
17/5	5.23	M	16.0	776S	CL	7
25/5	5.32	S	21.0	762R	CL	7
13/6	5.53	S	24.0	766S	CL	8
14/6	4.78	VL	22.0	767R	CL	6
14/6	5.53	VL	22.5	767R	CL	6
14/6	6.28	VL	22.5	767R	CL	5
14/6	6.86	VL	23.0	767R	CL	6
14/6	8.03	VL	22.5	767R	CL	5
14/6	8.61	VL	22.5	767R	CL	3
14/6	9.28	VL	22.5	767R	CL	4
14/6	9.78	VL	22.5	767R	CL	6
14/6	10.28	VL	23.0	767R	CL	5
16/6	9.45	M	18.0	769R	O/C	4
16/6	9.86	M	18.0	769R	O/C	1
16/6	10.36	M	18.0	770R	O/C	0
16/6	10.86	M	17.0	770R	O/C	1

Table E3b Number of singing male skylarks along a 1.25km transect on Offham farm. Counts along the transect were started every half hour from dawn (0600 hours) until 1730 hours on March 29, 1993. The maximum number of singing males was 15.

Time	No. singing skylarks seen
0600	7
0630	5
0700	10
0730	9
0800	12
0830	10
0900	12
0930	13
1000	15
1030	10
1100	9
1130	8
1200	10
1230	1
1300	6
1330	2
1400	4
1430	5
1500	5
1530	9
1600	4
1630	5
1700	2
1730	2