DEFRA EPG 1/5/188

Modelling the effects of farmland food webs of herbicide and insecticide management in the agricultural ecosystem

1 Summaries

Increasingly efficient agricultural technology, including the development of GM crops, and increasing concern over the well-documented declines of farmland birds has resulted in considerable debate about the future direction of agriculture. Informed debate would be greatly enhanced if it were possible to predict the ecological consequences of various management options. The aim of this report is to provide the theoretical framework for making such predictions and illustrate its applications. In this report we will both examine the opportunities available for making such predictions, the gaps in our knowledge and the opportunities for future research.

In this report we review the data on the diet and foraging ecology of farmland birds, review the information on weed population ecology based on six species of weeds and a range of different rotations, create models of weed populations with farmland birds and show how these models can be used to make predictions of the consequences of changes in agricultural practice such as changes in rotations, changes in the amount of winter stubble and the consequences of introducing HTGM crops.

Applying the models in this report to the data from the farm scale evaluations would be invaluable in predicting the implications of GM technology.

Objective 1. Foraging bird resource requirements and behaviour in conventional and alternative arable crop systems: a review of published research.

1.1 Introduction

The published literature on the resource requirements and behaviour of farmland birds in conventional and alternative arable crop systems is reviewed, concentrating on 21 selected species.

1.2 Food abundance

The availability of food to foraging farmland birds can be considered in terms of the abundance of that food and its accessibility. A good knowledge of the relationship between food abundance and species' breeding performance is needed for the deterministic model. Food abundance is shown to vary depending on crop type and crop management regime. Cropped areas generally have a lower diversity and abundance of invertebrates than non-cropped areas. Position within a field also influences food availability; invertebrates generally are more abundant at field edges compared to the centre.

Within non-cropped habitats, stubbles are an important winter food source for farmland birds. Under-sowing reduces seed density in stubbles. However undersown fields comprise an important food resource for invertebrate-feeding birds in the spring. The switch from spring-sown to autumn-sown crops has reduced stubble area and food availability for many birds. Set-aside generally has increased food abundance and availability compared to arable crops and grassland. Management regimes and enhancement (e.g. wild bird cover) of set-aside affect the availability of food on set-aside. The reduced pesticide applications on conservation headlands appear to positively affect food availability in most studies.

Modern practices relating to the increased intensification of farmland generally have an adverse effect on food availability. Frequent tillage, increased fertiliser usage, improved harvesting and storage of cereals, increased herbicide usage and the switch to autumn-sown crops all adversely affect broad-leaved weed populations. A few weed species may have increased as a response to some of these practices.

It is difficult to separate the effects of pesticides from other factors. However, it is generally assumed that the increasing use of pesticides in recent decades has had a detrimental effect on food availability for farmland birds. Many studies have found that insecticides reduce numbers of non-target arthropods, but this may be a short-term effect because of recolonisation from unsprayed areas nearby. Ewald & Aebischer (1999), however, did find long-term declines in many invertebrates over 30 years. Generally, increased herbicide usage is thought to reduce overall weed and seed abundance, and to reduce insect food availability, through the destruction of host plants. Fungicides seem to have reduced affects on invertebrate food abundance compared to herbicides or pesticides.

Integrated farming systems, with reduced chemical and nitrogen inputs, showed increased invertebrate populations compared to conventional farms, although these increases could also be attributed to other factors (Holland *et al*. 1994a). There is some evidence that the use of GM crops may lead to reduced abundances of weed seeds and invertebrates. Organic farms, in general, have greater food availability than conventional or integrated farms. This is probably due to a combination of factors including the prevalence of mixed farming, crop rotation, spring sown crops, the avoidance of agrochemical usage, the maintenance of non-crop habitats such as hedges and field margins, use of green manure, and cereal crop under-sowing.

Weather factors, such as rainfall, temperature and wind, can affect invertebrate food availability. Weather variables also interact with other factors such as pesticide effects to influence arthropod populations. Arthropods show a wide range of within-year and between-year variation in population abundance.

Resource-independent factors such as food accessibility and predation risk can also affect food availability, both of which are mediated by vegetation structure. There is evidence that food is less accessible and predation risk greater in uncultivated habitats (which have a greater winter herb biomass) compared to cropped habitats, and differences in preference for different crop types, such as spring cereals over winter cereals by foraging skylarks, may be due to density of vegetation/food accessibility factors.

1.3 Foraging behaviour

The published information on the relative use of farmland habitats (foraging preferences) is reviewed. Such data typically consist of comparisons between the numbers (or densities) of birds or time spent by individuals in a habitat, and the relative availability of that habitat. These studies involve either intensive field surveys or radio-tracking. Knowledge of a species' foraging preferences may give an indication of the relative availability of food between habitats, and so could theoretically be useful for the deterministic model. Knowledge of foraging preferences in terms of the behavioural response to differences or changes in food availability is also potentially useful for the resource limitation model. For either model, foraging preferences give an indication of where to sample food.

In general, farmland bird species are found to vary in their preferences for different crops or habitats. Preferences are generally determined by diet, and differ between winter and the breeding season. Radio-tracking studies tend to show that individual farmland birds spend much less than 50% of their time foraging in arable habitats compared to woodland, hedges and other semi-natural habitats. Insectivorous species tend to prefer permanent grassland, in particular grazed grass, and seed-eaters prefer stubble and sometimes set-aside. Winter cereal fields are almost universally avoided. Broadleaved crops and bare tilled soil are preferred by some species and avoided by others. Some studies show a preference of some species for oilseed rape over other crops, at particular times of the year. Within arable fields, most species tend to use the margins more than the centre. Estimates of food availability should take account of this behaviour. Information relating to the species being considered in this project is summarised.

Studies on the influence of pesticide applications on farmland bird distribution and behaviour are reviewed. There are few relevant studies, but field experiments with conservation headlands indicate that grey partridge broods preferentially forage in conservation headland areas, where broadleaved weeds and arthropod prey were more abundant. Blue-headed wagtails also foraged preferentially in unsprayed field margin strips. Foraging density of yellowhammers provisioning young was lower in crops which had received at least one insecticide application in summer than in those which had not.

The effect of changes in food availability on the consumption rate by farmland birds is described by the functional response. This differs between species and between food types and will also depend upon the range of foods available and the densities of those foods. It is clear that the net result of a decrease in the availability of a species' normal food will depend on the alternatives available; their relative profitability, density, handling time, predictability and crypticity as well as the individual's foraging ability and competitive ability. A good knowledge of functional responses of farmland birds is needed for the development of the resource limitation model.

A species' daily food intake can be predicted from a knowledge of its diet, bodyweight and digestive efficiency. Crocker *et al.* (2002) show that the results using this method are broadly in line with empirical data obtained using the doubly-labelled water method. Theoretically, therefore, avian energetics could be used in the modelling process, to relate changes in food availability in the farmland habitat to the food needed to meet a species' energy requirements. The use of empirically derived equations also allows the estimation of confidence limits on the predictions and it opens up the possibility of predicting not only the most likely food intake but also the unlikely or worst case scenarios. These methods, however, are based on several assumptions, and are subject to limitations. A considerable amount of further work is needed if avian energetics is to be useful in modelling farmland bird foods, reproductive performance and survival.

Objective 2 Predicting the response of farmland bird populations to changing food supplies

2.1 Introduction

Field trials, monitoring and experimental approaches are important tools for assessing the likely consequences of changes in farmland management for farmland birds. However, these can be conducted only on limited spatial or temporal scales. It is increasingly apparent that predictive modelling using computer simulations will prove invaluable as a tool for assessing novel management strategies. Here, we assess the options available for simulation modelling of farmland birds in relation to food availability. We focus on phenomenological models, including both aggregative and population models, and behavioural models.

2.2 Phenomenological models

These include both aggregative response models (relating numbers of foragers to the abundance of their food) and multi-factor population models (based on empirically determined rates of fecundity, survival and dispersal, and relating population sizes to a variety of aspects of the environment, including food supply).

Relatively few aggregative responses have been measured for farmland birds. If good relationships exist for a species, usually based on a single food source, then aggregative models can provide useful indications of how numbers of individuals using an area will respond to changes in their food supply (e.g. Watkinson et al., 2000). However, the utility of these models is restricted by difficulties inherent in their empirical measurement and, in particular, because they permit only limited inferences to be drawn regarding the response of populations to their food supply. If the availability of a favoured food species declines, foragers may switch to a different food source, or forage in different locations. Furthermore, aggregative responses measured under one set of circumstances may not be valid in a changed environment.

Few population models of birds link demographic rates explicitly to the availability of food. Two of the best known examples of this type of population model are those of great tits *Parus major* (Pennycuick, 1969) and grey partridges *Perdix perdix* (Potts & Aebischer, 1991) (see also Objective 10). This type of modelling has the considerable appeal of providing quantitative predictions of how an entire population might be expected to respond to a change in food supply within a given area. However, the data required to construct these models was collected over many decades. Such datasets are not available for other farmland birds. Indeed, few relationships between food availability and demography (the key requirement of these population models) exist for farmland birds (see Objective 11).

2.3 Behavioural models

For birds, behavioural models are typically parameterised for the non-breeding season and, as such, require less specific knowledge of the relationship between food availability and reproduction. Furthermore, by using simple approaches to estimate the food intake of foragers, relationships between food availability and mortality (a key regulating process) can be emergent properties of behavioural models.

These models can be either depletion based or interference based. Little is known about foraging interference in farmland birds, but neither disturbance or kleptoparasitism is likely to be a serious factor when dealing with small, non-motile food items (such as seeds), whilst direct aggression is likely to be a factor only during the breeding season. Consequently, depletion models are likely to be more appropriate for farmland birds than interference models.

Depletion models require that the intake of foragers is estimated. This can be done using functional responses, although for a variety of reasons, these cannot yet be estimated for farmland birds with any confidence (see also Objective 1). Simpler approaches employ well-established allometric relationships between body mass and energy requirements to estimate daily intake of foragers. Beyond the allometric relationships, these approaches require only that the critical density (the density of food at which foragers can no longer gain sufficient intake to sustain their energy levels) is estimated. This remains a poorly known parameter, although estimates for farmland birds range from 0.5 to $12.5kJm^{-2}$, with a modal estimate in the region of $5kJm^{-2}$.

Currently, the utility of behavioural foraging models is limited to the non-breeding season; breeding is typically incorporated using simple deterministic relationships (although, see Objective 7 for a framework for using behavioural models during the breeding season). Here, we suggest that this approach remains the most appropriate for modelling populations of farmland birds. Energetic flux models that can be used to predict over winter mortality of birds with individual variation are sensitive to energetic parameters, which are likely to be difficult to ascertain for farmland birds. Hence, we recommend the use of an iterative approach to determine the maximum number of individual birds that can survive the winter.

2.4 Conclusions

Of the approaches discussed, depletion models appear to have the greatest utility. For predicting population trends into the future, however, it is necessary to combine an iterative depletion model with a phenomenological model of breeding season dynamics based on empirical data. Bird diets appear quite flexible (see Objectives 3 and 5) and modelling competition and coexistence between species with broadly similar diets requires more information than is currently available. Thus, it is currently possible only to model certain types of birds with broadly different diets, to determine the likely consequences of a given change in the dynamics of resources for these broad groups.

Our review demonstrates that resource-based population modelling of farmland birds is severely limited by the availability of data. In particular, further research into aggregative responses, estimating critical food densities, and linking food supply to demography should be priorities within autecological studies. Gathering specific data on a greater range of species may allow more general rules to be discerned from species-specific approaches.

Objective 3. The importance of weed seeds as resources for farmland birds

3.1 Introduction

The value of a weed species as a food resource depends on its energetic value, as well as its abundance and availability in the agricultural environment.

Dietary information was collected for 22 farmland bird species; 12 of high conservation concern and three of medium conservation concern (Gregory *et al*., 2002), using 100 references from the United Kingdom and other European countries for which quantitative data was presented (Table 3.1). The number of studies and the detail available varied considerably between species (e.g. 11 studies on the rook *Corvus frugilegus* but only one for the stone curlew *Burhinus oedicnemus*). For some species dietary information is only available prior to agricultural intensification and may be unrepresentative of current feeding habits. These studies were, however, included because there would otherwise have been insufficient information for the ranking process.

3.2 Diet composition

Rankings were calculated separately for the plant and invertebrate components of the diet, however the ratio of plant to animal material reflects the relative contributions of each to a bird's nutrition and is important for assessing the overall importance of seeds versus invertebrates in the diet. Birds were classified into phytophagous, insectivorous or mixed species based on the ratio of plant to invertebrate components in the diet as reported in the literature (Table 3.2). Many adult birds show seasonal changes in the composition of their diet, with the proportion of invertebrate material being highest during the breeding season (e.g. quail, reed bunting, rook, skylark, tree sparrow). Adults and young often have quite different diets, and chicks usually consume a higher proportion of invertebrate material than adults, with the exception of the greenfinch and linnet (which are granivorous), and members of the Columbidae i.e. collared dove, stock dove, turtle dove, and woodpigeon (which are fed crop milk initially). For some species, chicks consume mainly invertebrates during the first few days and then switch to a diet of seeds later in the breeding season (e.g. goldfinch, grey partridge).

A range of investigative techniques were used to evaluate dietary composition (e.g. stomach contents, faecal analysis, neck collars, observation), however there are biases involved with each (Moreby 1988, Green & Tyler 1989, Brooks *et al.* 1995, Poulsen & Aebischer 1995, Moreby & Stoate 2000). Analysis of crop and stomach contents was the most commonly used method in this review, and this is thought to be the best method for evaluating bird diet as it has fewer biases than the other methods (Murton, Westwood & Isaacson 1964). Faecal analysis was frequently used to investigate the diet of chicks, although this may underestimate or exclude those species that become unidentifiable through digestion (Eybert & Constant 1992). Observation may be unreliable for identifying smaller food items, although this was usually only used in older studies.

Diet composition was measured in different ways, therefore studies were not always comparable (Appendix 3, Table 3.3). Percentage of items was most commonly used to describe the relative frequencies of food items, although this does not take into account the size of food items. Percentage biomass or volume was sometimes used for estimating relative amounts of seeds in the diet, however this was rarely used to estimate the invertebrate component of the diet. For several bird species, cultivated plants were the main (e.g. rook) or only food items (e.g. collared dove *Streptopelia decaocto)* and weed taxa could not be ranked.

Plant taxa were ranked in their importance for the 22 bird species, but because preferences vary between birds, also for individual species. Several steps were involved in ranking the taxa and full details of the methods used and results are given in Appendix 3, Sections 3.1-3.7. Rankings were determined separately for adult diet in the breeding and non-breeding seasons and for chicks (Table 3.4). Several patterns were apparent from the rankings. The most important plant families overall were Poaceae, Polygonaceae, Caryophyllaceae, Cruciferae, Compositae, Chenopodiaceae and Labiatae, although the latter two were unimportant for chicks. Similarly Boatman (2001) found that Poaceae, Polygonaceae, Caryophyllaceae, Chenopodiaceae, Compositae, Cruciferae and Labiatae (ranked in that order) were the most important foods. Similarities in dietary preferences were observed among some groups of birds (e.g. between finches (Fringillidae) and between members of the Columbidae (doves and pigeons) (Appendix 3, Section 3.1.3). Some bird species appeared to have a wider dietary range than others, however this may be a reflection of the taxonomic detail rather than the true dietary breadth. Moreover, the dietary information gained from each study is determined by the food available and this may vary spatially and temporally. However, regional differences in diet were not investigated in this review.

There was very little information on the calorific values of weeds that are important in the diet of farmland birds, and it was not possible to determine whether the nutritional value of seeds has a strong influence on food selection.

The relative abundance of weeds in the farmland environment is important for estimating the amount of food available to farmland birds. Ideally we need to know the typical densities of entire plants and seeds in order to estimate food availability, however this information was not readily available. Percentage cover was the most commonly used method, as it is an easy and quick way of estimating weed plant density, although plant cover may not be directly related to the abundance of entire plants or to seed production. Farm management practices (e.g. crop rotation, herbicide and tillage regimes) have an effect on weed abundance and diversity, and some of these factors were taken into consideration. There may also be spatial variation in the density of weeds within a field (e.g. Brown & Aebischer 2001, Wilson & Aebischer 1995), and the mean abundance of weeds was calculated separately for centre and edge positions. Data were compiled from several projects carried out in the United Kingdom (see Table 3.7), and this was used to estimate the typical densities of weeds in the farmland environment.

Bird species were categorised according to their preferences for foraging location within farmland (Appendix 3, Table 3.8). Some species show a clear preference for a particular foraging location (e.g. the skylark *Alauda arvensis* is considered to be a mid-field feeder), while others forage in a variety of habitats within farmland (e.g. cirl bunting *Emberiza cirlus).*

Preference for a particular taxon (rather than consumption) was not established as insufficient studies examined the availability of food resources along with presence in the diet. In order to determine *preference* for certain taxa, studies are needed in which presence in the diet is compared directly with availability at the foraging location. This has been attempted for a few species (turtle dove, skylark, grey partridge) providing in most cases an indication of preference.

Ideally, a final overall ranking of weed taxa would be determined for each bird species to identify which are the critical weed species for bird nutrition. However, this was not possible as there was insufficient information available for most of the bird species investigated in this project. The exception is the grey partridge *(Perdix perdix),* which has been the subject of many studies spanning a number of decades (e.g. Ford, Chitty & Middleton 1938, Hammer, Spärk & KØie 1958, Southwood & Cross 1969, Potts 1970, 1970b, Vickerman & O'Bryan 1979, Green 1984, Pulliainen 1984, Potts & Aebischer 1991, Itämies *et al.* 1996). Even so there is still insufficient information on the relative nutritional value of the most important weed seeds.

The functional responses of foraging birds to variations in invertebrate prey dependent on weed species are not known, but an initial step would be to examine the interactions between arable weeds and invertebrates that are important in the diet of farmland birds. However, interactions between arable weeds and invertebrates are highly complex, and this is an extremely large task. A literature search was carried out to examine relationships between weed taxa and invertebrate species. Some of this literature has already been reviewed by Brown (2001) and further information was added to this database.

Objective 4. Assemble available information on the dynamics of weed species seed populations over winter in arable fields

4.1 Introduction

The aim of this work was to assemble information that could be used to parameterise models for the population dynamics of arable weeds. These models then form the basis for the final simulation model (Objective 12). The changes in numbers of weeds from one year to the next are mainly dependent on (i) seed production of the weed; (ii) recruitment of new weeds from seeds in the soil; (iii) the influence of management on weed numbers.

This model parameterisation exercise focussed on 6 species of weeds. These were *Chenopodium album*, *Poa annua*, *Stellaria media*, *Fallopia convolvulus*, *Papaver rhoeas* and *Alopecurus myosuroides*. The first four of these are very important sources of bird food during winter (Objectives 3 & 5). The latter two are known to be of economic importance, but less important as food for farming birds. It was decided to include these species in order that the impacts of changing management could be predicted separately for species of economic importance as well as for species that are significant food resources for birds.

4.2 Methods & results

4.2.1 Seed Production

The literature yielded multiple estimates of seed production for all arable weeds within crops. To summarise, seed production in crops ranges from exceedingly high (c. 250 000 seeds per isolated plant), in the case of Chenopodium album to moderate (c. 200 seeds per isolated plant) in the case of Poa annua and Stellaria media.

As stated in our original objectives we set a priority on obtaining information for weeds growing in winter stubbles. We obtained information on seed production in stubbles from another DEFRA funded project. These indicated that weeds occurring on unsprayed stubbles were capable of producing small but significant numbers of seeds. Plants of *Chenopodium album*, for example, may yield an average of around 1500 seeds per plant, whereas plants of *Poa annua* may yield only 40 seeds per plant.

4.2.2 Seed bank dynamics

Information on rates of seedbank decay was collated from the published literature in order to yield estimates of how the numbers of weed seeds decline through time. Fig. 4.1*a* shows how the seedbanks of the 6 species in the modelling exercise decline through time in cultivated conditions. More informatively Fig. 4.1*b* shows how fast the seed output of a single plant decays through time. It is clear that the seed input will be extremely influential in determining how fast seed reserves are depleted through time. Species such as *Chenopodium album, Papaver rhoeas* and *Fallopia convolvulus* that produce large numbers of seeds will tend to persist for long periods in the soil even in the absence of further input.

We analysed published data on seedbank declines. These allow separate estimates of rates of seed germination and mortality that are fed into the final model for weed population dynamics (Objective 12).

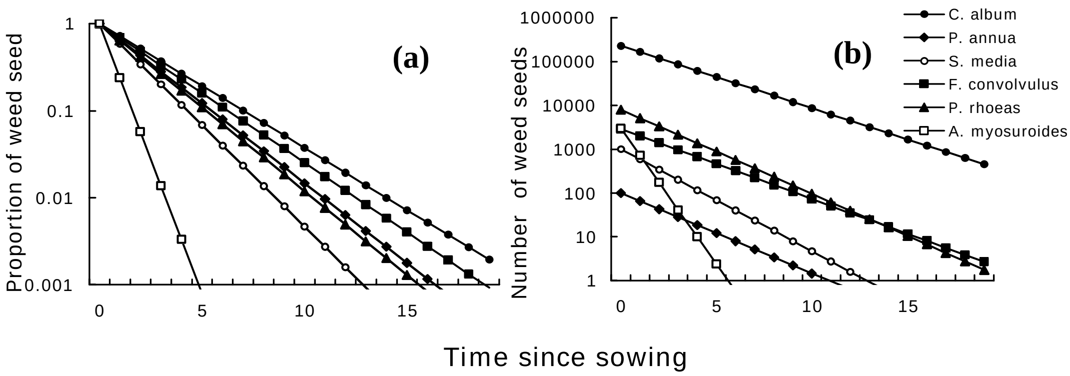

Fig. 4.1 The long-term dynamics of seedbanks of arable weed species. (a) The poportion of seeds remaining following an initial sowing. (b) The total number of weeds remaining following the seeding of a single plant.

4.2.3 BASELINE DENSITIES AND MANAGEMENT

We combined information from 2 sources. Firstly, information was supplied by ADAS on the efficacy of control of weeds in different crops. Secondly, we used estimates of densities from the IFS dataset. Taken together these yielded baseline information on the control of weeds in the crops considered in the models (Table 4.1).

	Winter wheat		Winter rape		Sugar beet		Spring barley		Peas	
Species	herbicide control	Ranking	herbicide control	Ranking	herbicide control	Ranking	herbicide control	Ranking	herbicide control	Ranking
Polygonom spp.	>95%	easy	100%	-	95%	Moderate	50-95%	difficult	50-80%	awkward
Chenopodium album	>95%	easy	100%	-	95%	Moderate	>95%	awkward	95%	easy
Senecio vulgaris	>95%	easy	95%	easy	90%	moderate	>95%	easy	95%	easy
Poa annua	100%	v. easy	90%	easy	95%	moderate	30-95	awkward	80%+	easy
Stellaria media	100%	v. easy	90%	easy	100%	easy	>95%	easy	80%+	easy
Alopecurus myosuroides	90%	moderate	95%	easy	95%	easy	40-80%	difficult	-	-

Table 4.1 Summary of information on the relative ease with which weeds are controlled in different crops, together with typical proportions of weeds killed by herbicide application.

4.2 Summary

The information collated yielded parameters that were fed into models for the population dynamics of the 6 species of weeds in conventionally managed systems. These models then form the basis for the final modelling exercise (Objective 12).

Objective 5. The importance of invertebrates as resources for farmland birds

5.1 Introduction

There are a number of steps involved in ranking the importance of invertebrate food resources and these are listed below (Sections 5.1-5.6). The methods used were the same as for Objective 3 (see Appendix 3, Section 3.1) and the results are given in Appendix 5.

The degree of taxonomic resolution varied considerably between studies, making it difficult to create rankings for invertebrates. A few references listed taxa to species level, but the majority identified invertebrates only to the level of Order. The difficulty in identifying invertebrate fragments was probably a limiting factor, as was the entomological knowledge of the researchers. Because individual species were not identified in most studies, analysis was not possible at this level and importance rankings could be determined only for invertebrate Orders. Considerable variation exists between the size and consequently nutritional value of invertebrates at this level of taxonomic resolution therefore the results have limited value. Moreover, because individual insect species vary considerable in their habitat requirements predictions as to the likely impact of changes in farming practices on farmland bird diet cannot be made unless this is available.

5.2 Diet composition

The most important invertebrate Orders overall were Coleoptera adults, Hemiptera adults, Arachnida, Lepidoptera larvae/pupae, Diptera adults, Lepidoptera adults, Diptera larvae/pupae, and Hymenoptera[1] adults (see Table 5.2). However, Lepidoptera adults, Hymenoptera[1] adults, and Arachnida were not important food items during the non-breeding season, when a smaller number of invertebrate taxa were important (only 11 taxa, cf. up to 28 taxa in the breeding season).

The invertebrate component of the diet of adults and chicks during the breeding season was examined using correspondence analysis. Similarities in dietary composition were observed among closely related bird species e.g. the grey and red-legged partridge chicks had similar diets, as did members of the Emberizidae.

There was very little information on the calorific and nutritional values of farmland invertebrates in general, and almost none on the digestibility of different body parts. There is a need for further research in this area, particularly on invertebrates that are important food items for declining bird species, as it would increase our understanding of the factors that determine prey selection and dietary preference. Moreover such information is needed if we are to understand the impact of farming practices that change invertebrate composition.

There is very little information on the relationship between the abundance of invertebrates in the field and bird dietary preferences, and very few studies compare the presence in the diet with availability at bird foraging locations. As with weed seeds, it is difficult to measure the availability of invertebrates as food items because we need to sample the areas where birds are actually foraging, and this may not be known. Even for well-studied species such as the grey partridge "the real availability of the invertebrate taxa for grey partridges is difficult to verify, since very little is known about how efficiently chicks can find and catch different prey items in different habitats" (Itämies *et al.* 1996). The lack of information meant that it was not feasible to rank the importance of invertebrates in relation to their availability.

Objective 6. Sampling and data recording techniques applicable to questions concerning bird food resources.

6.1 Introduction

This section aims to review the published literature on sampling methods used to estimate density or biomass of bird food/prey items in order to assess: (a) the repeatability of the estimates obtained using the different methods; (b) the extent to which the methods measure food availability and (c) the extent to which methods can be standardised, in order to include such data into the models proposed in this project.

6.2 Review of methods

The most commonly used techniques for measuring the abundance of plants and arthropods are listed, and summaries given of their known efficiencies and limitations. Interception traps, vacuum nets, sweep nets, knock-down, visual counts, mark-release-recapture, attraction, emergence traps and soil cores are considered for measuring arthropod abundance. Density, cover, biomass or yield, basal area and frequency are considered for measuring plant abundance. Various techniques for measuring vegetation structure and seed abundance are also described.

The particular techniques which have been used in studies of farmland bird food resources are then reviewed with a view towards standardisation. A wide variety of methods are found to have been used, governed mainly by the species of bird being considered and its foraging behaviour and habitat. Other considerations include cost, staff resources and time. The methods vary in terms of their efficiencies and probably repeatability, though few data are available on the latter. Also, different methods are affected in different ways by external factors such as vegetation structure and climatic conditions. It is therefore very difficult to compare the results of different studies, and to combine their data when constructing models.

Generally, methods measure relative rather than absolute abundance and this becomes important when attempting to compare the amount of food available to the amount of food needed to survive or reproduce (see Objective 1). More work is needed, therefore, on the efficiencies of the different methods, and hence the calibration coefficients to convert relative to absolute abundance for each device used.

Farmland bird species can be divided into guilds based on their diet and foraging behaviour. When this is done for the species being considered in this report, we are able to suggest standard methods for assessing food availability for each guild (the process is summarised in Table X). Method selection was based on the frequency by which the methods have been used in previous studies, as well as efficiency and any data on repeatability. Cost and ease of use were also taken into consideration, although these were regarded as being of secondary importance.

6.3 Summary

Further work is needed on the repeatability and efficiency of most of the methods reviewed in this Section, in particular the D-Vac method and sweep netting.

Table 6.1. Suggested standard methods for the measurement of food availability for farmland birds.

Diet	Foraging behaviour	Recommended standard method
Seeds	Mainly forages on ground	Count of surface seed using 0.25 m^2 quadrats
Seeds	Forages on ground and by disturbing surface	Removal of top 1 cm soil, followed by separation and counting of seed
Seeds, plants and/or fruit	Forages on ground, disturbs surface and searches plants and trees	Removal of top 1 cm of soil and vegetation, separation and counting of seed and fruit and weighing of plants For trees, count seed or fruit in situ
Invertebrates	Mainly forages on ground	D-Vac
Invertebrates	Forages on surface and below ground, e.g. by digging	Removal of vegetation and 1-5 cm of soil surface (depth depending on bird species), separation of inverts into groups and weighing
Invertebrates	Caught on the ground and on the wing	D-Vac + sweep net

Objective 7 Extend the depletion models to apply to the breeding season

7.1 Introduction
Depletion of food resources acts to limit the number of individuals that can use an area, as depletion is related to the density of foragers (Sutherland & Anderson 1993). Such models have been used to predict the number of individuals able to use an area, but their use has generally been restricted to the non-breeding season.

7.2 Model framework
In the breeding season two extra processes need to be incorporated, resource renewal, for example insects can hatch at a rapid rate, and birds have to provide for their young. It is also necessary to distinguish between species with altricial (young stay in the nest) and precocial (young leave the nest) young. Here we construct an outline framework showing the principles that would need to be developed to construct models linking food resources to reproductive output and breeding population size. We do this separately for altricial and precocial species.

For both altricial and precocial species, many of the key parameters required to parameterise the models were not available. However, it was in principle possible to construct such models in such a way that the impacts of agricultural management decisions could be traced through invertebrate densities to avian reproductive success.

We identified the key gaps in our knowledge where further research is required to effectively implement such depletion models. These were: 1) Invertebrate distribution and local rates of population change through the season, 2) detailed dietary requirements of chicks in relation to prey availability, 3) Details of functional response parameters and 4) Chick growth responses, particularly in relation to subsequent survival.

Objective 8 Identify further work on functional responses

8. Work required for the wider applicability of functional response models

The functional response is the relationship between forager intake rate and food density (Solomon, 1949). For foragers feeding in habitat containing patches with a range of food densities, functional responses may be used to predict the distribution of foragers between available patches, the rate at which the foragers consume food in each patch and, consequently, the number of forager-days that the habitat can support. As a result, functional responses have formed the basis of many behaviour-based foraging models, most commonly for wading birds (e.g. Gill et al., 2001; Goss-Custard et al., 1996; Stillman et al., 2000; Sutherland, 1992, 1996). They are also essential for deriving estimates of the critical density, the density of food at which foragers can no longer obtain sufficient food for survival.

Unfortunately, very few functional responses have been measured for farmland birds and other granivores (see Objective 2, section 2.3.2.2). Those that have been measured illustrate the current uncertainties in using functional responses for modelling foraging in farmland birds. Specifically, the examples summarised in Table 2.1 show that for granivores, estimates of search efficiency (one of two key parameters required to estimate the functional response) vary by three orders of magnitude. Measurements of the functional response may be affected by the size of the food item, the size and morphology of the foraging species, the nature of the substrate, the minimum food density at which foragers are observed to feed, the position of birds within a flock, the period of time over which experiments are conducted, and the condition of the birds when data are collected (see Objectives 1 and 2).

The principal weakness of functional response models presently arises from the lack of estimates available. In order for such models to be more widely applicable, it is essential that further estimates are obtained, both by observing how intake rate varies in patches of naturally varying resource density, and by experimental provisioning with different densities of resource. Such measurements should be a key aim of autecological studies.

Objective 9. Methods for applying the depletion model at a greater spatial scale and at a community level

9.1 Introduction

A model parameterised for a single species of forager, feeding on a single resource, can be used to infer the potential consequences of changes in farmland management for that species (Watkinson et al. 2001). Such a model is a greatly simplified representation of the rural landscape. This is partly to its advantage, in allowing relationships between changes in management and population responses to be elucidated clearly. However, the simplicity of the model might also be viewed as a weakness: the variety of factors interacting in the real landscape may confound the relationships identified by the model, and few species interactions are as straightforward as one forager feeding on a single resource. In order to provide a greater understanding of the variety of interactions occurring within a real arable landscape, it would be useful to apply a model at a community level, on a landscape scale. For a depletion model based on farmland birds feeding on a variety of resources within the arable landscape, therefore, several processes should, ideally, be parameterised. These include modelling a variety of weed and invertebrate species; increasing the model landscape to involve a larger variety of the variation found in the real landscape (for example, a diversity of crop rotations and weed management systems); and incorporating a diversity of foraging species.

9.2 Modelling a diversity of weeds and invertebrates

Adapting existing models to incorporate a diversity of weeds presents no serious problems. Good information exists on the population dynamics of many arable weeds (see Objective 4) and these can often be modelled using the same framework. Interactions between weeds are negligible relative to interactions between weeds and crops, so many weeds can be incorporated into a single model, without adapting parameters to account for the presence of other weed species. Weed dispersal between fields is not well understood, however. To account for this a small rate of immigration can be included in a large scale model.

Unfortunately, a variety of invertebrate prey cannot be so readily included. This is because much of the data required, especially about invertebrate population dynamics, are lacking. Invertebrates, particularly during the breeding season, may be a constantly renewing resource but we do not fully understand the density-dependent or density independent processes that determine the rates of production (see Objective 7). With current knowledge, this restricts the application of a broader-scale depletion model to granivores and, consequently, dictates that depletion modelling for most farmland birds is restricted to the non-breeding season.

Modelling foraging when a variety of food sources are available, is reasonably straightforward using optimal, functional response approaches. However, it is unlikely that the functional response approach is currently applicable to many farmland birds (Objective 2). If food preferences can be ascertained with accuracy, resources can be removed from the environment acording to some weighted index of availability and preference. However, many farmland birds have quite flexible diets and preferences would be very hard to determine from available data (see Objective 3 and section 9.4, below). Thus, at present, simulations that allow foragers to remove food within their dietary scope, in direct proportion to its availability, are likely to be the best method.

9.3 Incorporating variation in landscape management

In reality, a huge number of factors affect the management of individual fields within farms. typically, however, these factors result in variation in three aspects of management. First, the order in which crops are grown in the field may vary. In models, it is possible simulate this by assigning each field one of a range of typical crop rotations, such that dates of sowing and harvest for that field, and levels of weed control within it, will vary each year depending on the stage of the rotation that it has reached. Second, the efficacy of weed control may vary according to the management of a field. This can result from different weather patterns, soil conditions or, even, from social factors affecting farm management. Crucially, however, it manifests as variation in weed control between fields and years. It is possible to simulate this by drawing weed control parameters randomly for individual fields, from a distribution with an appropriate mean and variance, to produce a realistic diversity of weed densities. Finally, decisions about whether to cultivate a field before winter may also vary from year to year. The simplest way to incorporate this into a simulation, is to make cultivation a stochastic process with a given probability. In the future, it might also be useful to determine whether there are patterns in cultivation, such that certain fields have a greater chance of being left uncultivated than others.

9.4 Incorporating a community of foragers

To apply depletion models at the level of a farmland bird community poses many problems. Dietary divisions between the majority of species are indistinct (see Objectives 3 and 5) and assessments of a single species' diet vary markedly according to methodology, year, timing and location of studies. The former confounds attempts to classify the diet of a species exactly, whilst the latter indicates that most species have some flexibility of diet to reflect what is available. Thus, it may be possible only to model certain types of birds with broadly different diets, to determine the likely consequences of a given change in the dynamics of resources for these broad groups (see Objective 2).

9.5 Conclusions

Available data permit the model to be extended to include a diversity of weed species, and to incorporate a variety of management processes, leading to a wide range of habitats in the landscape. Unfortunately, availability of data on density dependent processes in invertebrate dynamics limit the inclusion of invertebrate feeding in the model. Similarly, current knowledge is inadequate to allow the inclusion of a wide variety of competing, coexisting species of foraging birds in the model. Further information on both of these issues is necessary to extend the model to fully encompass the farmland foodweb.

Objective 10. Empirically based modelling approach linking food abundance, breeding performance and population status

10.1 Introdution

Changes in agricultural practice have been implicated in the declines of many farmland bird species through the effects they may have on food availability. The grey partridge (*Perdix perdix*) provides the best documented case study of such effects. In this section a simple, empirically-based modelling approach to estimating the likely consequences of agricultural change on farmland bird populations is presented, using the grey partridge as an example. The aim is to produce the simplest structure required to link food abundance, breeding performance and population status to allow comparisons of the value of different agricultural strategies to this species. We then consider the wider application of this approach, using the corn bunting (*Miliaria calandra*) as a case study of a passerine species.

10.2 The model of grey partridges

A generalised stochastic difference equation model was constructed to evaluate changes in the use of pesticides on the survival of the grey partridge, via effects on invertebrate chick food. The model runs on one-year time steps, with an arbitrary initial population of 100 adult birds. From the initial 100 birds the number of chicks hatched is calculated, followed by their survival to 6 weeks of age. This was the only stochastic element of the model, so that the overall variation in the final result was not influenced by the stochasticity of parameters that were not subject to adjustment. Insect abundance was then adjusted (increased) in line with field measurements for areas with modified spray regimes according to the "conservation headland" prescription. This was modelled by increasing the annual chick survival in line with the following regression equation (Aebischer, pers. comm.):

$$\text{Chick survival (probit)} = \text{Insect abundance} - 0.665 * 0.399 + 0.889$$

This equation was derived from data on invertebrate abundance and chick survival collected during the Game Conservancy Trust's long-term monitoring study of cereal ecosystems in Sussex. Insect abundance was expressed as an index, incorporating weighted estimates of the numbers of groups known to be important in the diet of grey partridge chicks. Actual survival probability was calculated from the probit survival rate. The number of chicks surviving to 12 months of age, and the adult survival rate were then applied to calculate the next year's adult population size. The model was run for 25 years and the mean chick survival rate (s) and population growth rate (r) calculated over this time interval. Sufficient simulations (3000) were run to ensure that the results were precise to two decimal places, i.e. further simulation would not change the values given. Increases in insect abundance of the order recorded in studies where pesticide input was reduced produced substantial changes in the population growth rate r, with values ranging between 0.03 and 0.49 for the examples given.

To construct an empirical relationship between chick survival (CSR) and population change, National annual chick survival figures were obtained for the period 1962-1993 from the Partridge Count Scheme of the National Game Census, and national annual estimates of breeding partridge abundance were obtained from the British Trust for Ornithology's published Common Bird Census for the period 1962-1993. The resulting relationship is given by the following equation:

$$N_{t+1}/N_t = 0.301 + 1.995 \text{ CSR} \quad (r=0.826, 30 \text{ d.f.})$$

where N_t = population in the first year and N_{t+1} = population in the second year

Increases in insect abundance of the order recorded in studies where pesticide input was reduced produced changes in the population growth rate (Nt+1/Nt) of between 0.880 and 1.378, with the majority being greater than 1, i.e. indicating a population increase. The threshold value of chick survival rate i.e. the value at which numbers remained static, was 0.35.

The model framework demonstrates how quantification of the effects of food abundance on partridge chick survival, together with the effects of chick survival rate on trends in partridge abundance allow food abundance to be related to population status. The model presented only accounts for changes in partridge numbers between two years. Longer term population changes are influenced by a wider range of density dependent and independent factors.

10.3 Summary

In principle, the model devised for the grey partridge may be applied to other farmland species with some modifications. As an example, elements of a model for corn bunting were prepared. The relationship between the probability of a corn bunting brood surviving to fledging and the corn bunting food index was modelled using data from the Sussex corn bunting study (Brickle, *pers. comm.*) and a binary logistic regression procedure. Predicted values of the probability of brood survival to fledging varied from c. 0.5 to > 0.9 over the range of food abundance values measured, suggesting that arthropod abundance in the vicinity of the nest had a significant effect on the survival of broods. Methods of extending this model to predict population change are discussed.

Objective 11. Work needed to extend the range of bird species that can be covered by deterministic models

11.1 Introduction

The deterministic (empirically-based) modelling approach requires information on the relationships between: a) food abundance and breeding parameters and (b) performance measures and population status, for a range of farmland bird species. It is known that this information exists for the grey partridge (*Perdix perdix*). Further work has recently been completed on a number of other farmland bird species. This section aims to produce a matrix of declining farmland bird species and datasets describing food availability, annual productivity and population change, to assess the suitability of the datasets for the analytical framework proposed under Objective 10, and to indicate the studies required to fill the gaps.

11.2 Review of data sets

Each study was examined to determine the type of data collected, the sampling method used and the parameters included in any population model. A matrix was drawn up summarising the availability of datasets, and each dataset was then evaluated individually. A summary of the matrix is given below (see appendix for further details). No suitable datasets were found for cirl bunting, collared dove, quail, rook, stone curlew, tree sparrow, woodpigeon, or yellow wagtail.

Table 11.1 Farmland bird species and published papers relating breeding performance to either food availability or population size.

Species	Food availability & annual productivity	Annual productivity & population change
Chaffinch		√
Corn bunting	√	√
Goldfinch		√
Greenfinch		√
Grey partridge	√	√
House sparrow		√
Linnet		√
Red-legged partridge	√	
Reed bunting		√
Skylark		√
Stock dove		√
Turtle dove		√
Yellowhammer		√

Few studies have examined relationships between chick food availability and productivity. Studies of other species have been carried out in which both food abundance and productivity have been assessed, but not related to each other (e.g. skylark and yellowhammer). It is hoped that examples of such relationships may be established from data collected during the ongoing DEFRA-funded study on "assessing the indirect effects of pesticides on birds" (PN0925).

Measurement of breeding performance is not always straightforward. In the examples modelled in the previous chapter (grey partridge and corn bunting), there was a significant relationship between chick food availability and chick survival. However, absence of such a relationship does not necessarily mean that there is no effect, nor that altering pesticide use may not result in a change in the population. Chick condition may be affected which may influence post-fledging survival. Chick quality is also difficult to measure, and brood reduction (i.e. loss of one or more chick) may affect the performance of remaining chicks, thus masking any measurable effects on individual chick performance. Alternatively, parents may have to work harder to feed their young under conditions of low food availability, which may affect their own condition and hence chances of survival over the following winter.

The ideal measure of productivity is the number of young produced per pair (or per female). Grey partridges and most corn buntings are single-brooded. However, most other species in Table 11.1 are multi-brooded. Lack of data on total annual productivity does not invalidate the application of the empirically-based modelling approach, but if there is an interaction between outcomes of first and second (or later) broods, this could confuse the interpretation of results based on single nests.

Studies relating productivity to population change are available for a greater range of species, however these are not always ideal for incorporation into the modelling approach adopted here. Demographic models for several species indicate that breeding performance per attempt was higher while populations declined. However, these models do not allow for density dependence. In a declining population, it is likely that sub-optimal habitats will be vacated first, which may improve resource availability on average for the remaining birds, thus potentially increasing productivity. It would be advantageous to carry out further analyses of the BTO's extensive datasets incorporating density dependence. However, the modelling approach used in section 10 only estimates the population change from one year to the next, thus approximating to a population in equilibrium and discounting most of the additional factors which influence outcomes over longer periods.

Objective 12. A landscape model of arable farmland: implications for the impacts of agricultural management on farmland birds

12.1 Introduction

We present a large scale simulation of bird species foraging in an agricultural landscape. Using this model we simulate three kinds of management changes: (i) varying the proportions of land under different types of rotation; (ii) changing the proportions of land left as stubble over winter; and (iii) the use of GMHT winter rape and sugar beet. These scenarios encompass a range of current and potential future farming practice, and we use the results of the model to consider the following questions: (i) To what extent do variations in current farming practice impact on biodiversity? (ii) Can declines in biodiversity be ameliorated by simple changes to current practice, such as ICM (integrated crop management)? (iii) What are the likely impacts of future changes, particularly the impacts of GMHT crops?

12.2 The model

12.2.1 CROP ROTATIONS AND WEED DYNAMICS

The model works at the scale of individual fields on an area of 15 ha comprising 300 fields. We incorporated 3 main rotations, (i) winter oilseed rape – winter wheat – winter wheat; (ii) sugar beet – spring barley – spring peas – winter wheat; (iii) spring barley – winter oilseed rape – winter wheat. The dynamics of six arable weed species were modelled. These were fat hen *Chenopodium album*, annual meadow grass *Poa annua*, chickweed *Stellaria media*, black bindweed *Fallopia convolvulus*, poppy *Papaver rhoeas* and blackgrass *Alopecurus myosuroides*. A review of bird diets (see Objectives 3 and 5) indicated that the first four of these were important sources of bird food during winter, whilst the latter two are known to be of commercial importance, due to their influence on the herbicide management of fields.

The models for the weeds were based on parameters estimated in Objective (4). The time step of the model was a single week, allowing flexibility in the timing of management in different crops, as well as differential phonologies of different weed species. The key time points in the model are crop sowing, weed emergence, herbicidal control, weed flowering and seed set, and the input of seeds into the seed bank. We also incorporated the possibility for weeds to germinate and set seed in winter stubbles.

In order to ensure a realistic range of densities for each weed three separate scenarios were developed, with different mean levels of control for each weed. This permitted the effects of changes in management to be predicted independently for *clean, 'normal' and weedy farms, or for areas of each of the three scenarios to be combined within a single landscape, to reflect a realistic diversity of weed densities at the regional scale.*

12.2.2 BIRD FORAGING AND POPULATION DYNAMICS

In the model two species included, based broadly on two contrasting farmland passerines. These were the skylark *Alauda arvensis*, with a body mass of approximately 38g and a preference (among the weeds modelled) for the seeds of fat hen, and the cirl bunting *Emberiza cirlus*, with a body mass of 23.5g and an preference for seeds of annual meadow grass, chickweed and bindweed (see Objectives 3 and 5). Bird foraging was modelled explicitly only during the non-breeding season, based on daily energy requirements.

12.2.3 MANAGEMENT OPTIONS

To generate predictions of how weed and bird populations will respond to changes in agricultural management, three simple aspects of management could be varied within the model. These were the proportions of different rotations, the probability of fields being left uncultivated over winter, and the use of GMHT rape and sugar beet. Control of weeds within GMHT crops is known to be very high and often complete (Watkinson et al., 2000). To model the use of either GMHT rape or sugar beet, control of all weeds in these crops was set to 100%.

12.3 Results

12.3.1 WEED DYNAMICS AND RESPONSES TO AGRICULTURAL MANAGEMENT

Simulations that changing the proportion of the different rotations has a surprisingly limited effect on weed dynamics. In the standard scenario (Fig. 12.7), few patterns are evident, even when increasing the proportion of any of the rotations up to 75% of the total area.

Fat hen and poppy were predicted to be largely unaffected by the proportion of overwinter stubbles; annual meadow grass, chickweed and bindweed populations are positively dependent on the proportion of stubbles; and blackgrass actually appears to be negatively affected by stubbles. Areas with low weed densities are highly affected by changes in the amount of uncultivated land over winter, as control in these areas is high and weed populations are dependent on survival in areas of uncultivated, untreated land. In contrast, weedy areas are poorly controlled and weed populations are unlikely to benefit greatly from the opportunity for reproduction over winter.

Fat hen is predicted to be the main weed negatively affected by the introduction of GMHT beet (Fig. 12.15b). By contrast, all other weeds are negatively affected by the introduction of GMHT winter rape (Fig. 12.15a). When both GMHT beet and GMHT rape are introduced, all of the weeds decline, with both fat hen and chickweed approaching extinction within 50 years of simulation.

12.3.2 RESPONSE OF FARMLAND BIRD POPULATIONS TO AGRICULTURAL MANAGEMENT

Farmland birds are often highly aggregated on very rich resources and populations are quite dependent on the proportion of fields with very high food densities, rather than on the overall mean.

The consequences of changing the proportion of uncultivated stubbles are qualitatively similar for the two species but far more pronounced for the more generalist cirl bunting. Switching to a system with no overwinter stubbles leads to a 40 to 50% decline in skylarks. By contrast, the same change in management leads to an abrupt decline in cirl buntings and extinction well within 50 years.

12.3.3 Response to the use of herbicide tolerant crops

The introduction of GMHT crops had very different consequences for the two dietary groups of birds (Fig. 12.22). Skylarks showed very little response to the introduction of GMHT rape. By contrast, the consequences of introducing GMHT sugar beet were extremely severe, with a rapid decline, and extinction of the skylark within 20 years. This contrasts with the cirl bunting, which showed little response to the introduction of GMHT beet, but severe consequences arose as a result of the use of GMHT rape.

12.3.4 Amelioration of GMHT crop use

It has been suggested that such is the control of weeds in GMHT crops, that there is less need for weed control when the crop is not in the ground. It is possible, therefore, that the effects of GMHT crop use could be ameliorated by the increased prevalence of land left uncultivated over winter. The effects of the simultaneous switch from a 5% to a 10% stubble regime and the introduction of GMHT crops on the population densities of farmland birds predicted benefits of the increased prevalence of uncultivated land to cirl buntings which far outweigh the damage done by the introduction of GMHT crops. However, the same is not true for the skylarks, which decline as precipitously even when stubble frequency increases.

12.2 **Summary**

In summary the model results suggest the following:

(1) Impacts on weeds of varying current rotational practice tend to be small, and impact only on one or two of the species modelled (typically spring germinating broad-leaved weeds).

(2) Introducing stubbles has countervailing impacts on weeds. Some weeds populations respond positively, some negatively, and others are unaffected.

(3) The effects of GMHT crops on weed densities depend on the nature of the rotation and weed species present. Most weed species will respond negatively, and declines are predicted to be severe for low density populations.

(4) The negative effects of GMHT crops can, in some cases, be ameliorated by increasing the proportion of winter stubbles.

(5) The response of bird populations depends on life-history. Species specialising on small seeded broad-leaved weeds, such as skylarks feeding on C. album, would be expected to be strongly negatively affected. Birds feeding on more generally occurring weeds, such as cirl buntings, may be less negatively affected.

The model we have presented may readily be modified to consider alternative rotational practice, and a range of farming systems, and further weed and bird species.