Predicting the response of farmland bird populations to changing food supplies

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Summary

1. Agricultural developments over recent decades have had significant negative effects on wildlife. Modern European agriculture faces many further developments in technology, finances and climate. A framework for predicting the consequences of these developments and for informing management that mitigates previous depredation of wildlife is essential.

2. Field trials, monitoring and experimental approaches are all invaluable tools for predicting the consequences of proposed agricultural practices. However, such trials are time-consuming and expensive, with limited spatial and temporal scope. Increasingly, it is recognized that predictive modelling using computer simulations is essential for assessing the likely impacts of novel management practices.

3. Many agricultural developments are likely to have impacts on the availability of food for farmland wildlife. In this paper, we review modelling techniques that are available for predicting the consequences of changing food supplies for farmland birds, a group already shown to be sensitive to agricultural management.

4. We focus on two broad types of simulation modelling: phenomenological approaches (using aggregative responses or full population models), and behavioural depletion models (including daily ration and functional response approaches). We assess the strengths and weaknesses of each, particularly with regard to available data.

5. We conclude that given the constraints on current information, daily ration models probably represent the most useful form of simulation modelling for farmland birds. Few phenomenological population models link demography explicitly to food supply and collecting data on these links should be a priority of autecological studies. More empirical data on aggregative and functional responses is needed to identify the generality of these functions, and to confront uncertainties in their use.

6. Synthesis and applications. Modelling techniques available for predicting the consequences of changing food supply for farmland birds have largely outstripped the availability of data required to parameterize them. We recommend the best available techniques given current constraints on data. Predictive models of biodiversity response should be more widely used when considering proposals for agricultural developments or agri-environment schemes. Models will provide a basis for selecting between competing proposals, whilst their widespread usage will both permit more frequent model validation and aid in model development.

Key-words: aggregative responses, functional responses, population models, behaviour-based modelling, granivorous birds.

Introduction

Many species of birds associated with farmland have undergone significant declines and range contractions during past decades (Fuller et al. 1995; Siriwardena et al. 1998). There has been a growing awareness that these declines are linked to changes in agricultural practices (O’Connor & Shrubb 1986; Krebs et al. 1999; Chamberlain et al. 2000; Robinson & Sutherland 2002; Benton, Vickery & Wilson 2003). Specifically, five mechanisms have been linked to farmland bird declines (Chamberlain 2002). These are the increasing use of autumn sown cereals, increasing specialization and loss of crop diversity, increasing density of vegetation arising from increased fertiliser use, increased livestock density, and agricultural improvement of pasture, with consequent loss of rough grazing. Together with changes in herbicide management (Potts & Aebischer 1995; Wilson et al. 1999; Watkinson et al. 2000) and the loss of hedgerows (Bradbury et al. 2000; Kyrkos, Wilson & Fuller 1998), these factors are likely to have had negative impacts on the availability of food and other resources (notably nest sites) for farmland specialists.

Recognition of the causes of farmland bird declines is an important first step towards reversing these trends. In order to assess the management options available for subsequent action, it is necessary to have methods for predicting the consequences of different strategies for farmland bird populations. Such methods are also needed to predict the consequences of implementing novel agricultural techniques, or of changes in the environment. Clearly, field trials (e.g. Firbank et al. 2003), monitoring and experimental approaches are important tools for making such predictions (Sutherland & Watkinson 2001). Such trials, however, can be conducted only on restricted spatial or temporal scales and are of limited use in a predictive context. In order to inform fully our understanding of their likely impacts on farmland bird populations these approaches must be augmented by other tools. In such situations, predictive modelling using computer simulations is also likely to prove invaluable as a tool for assessing novel management strategies.

Predictive models for birds in changing environments have been reviewed recently by Norris & Stillman (2002). These authors distinguished between, and focused on, population viability analysis (PVA) and behavioural modelling. PVA is used to assess the risks of extinction faced by populations and to examine the sensitivity of such risks to different types of management intervention. Behavioural models are those in which the behaviour of individuals is based on some form of optimization criterion. There are no guidelines on what constitutes a valid PVA and details will depend on the extent of available data (Boyce 1992). Clearly, however, PVA can vary from simple, deterministic matrix models, to complex individual-based models (Beissinger & Westphal 1998), whilst behavioural models can, themselves, be used to look at risks of population extinction under different forms of management (e.g. Stephens et al. 2002). Therefore, rather than being a type of modelling, PVA describes the application of any form of population model to looking at extinction risks.

In this review, we analyse models available for predicting the likely effects of changes in food availability on farmland birds. Specifically, we are interested in predicting the value of farmland as feeding habitat, and the consequences at a population level of a change in this value. We focus on two broad classes of models that have been, or may be, used to assess the impacts of changing food supply. These include phenomenological models (including both aggregative and population approaches) and behavioural depletion models (both daily ration and functional response approaches). We assess the strengths and weaknesses of each approach, the conditions under which their use would be appropriate and the types of predictions each would allow. In addition, we assess the crucial deficiencies in data that limit the application of available models.

Phenomenological models

Phenomenological models are based on direct experience, i.e. empirically determined relationships between populations and their environments. If conditions remain within the range over which the model was parameterized, then it is possible to predict aspects of the population’s response on the basis of established relationships. Phenomenological models of use in the current context range from simple, aggregative response models (relating numbers of foragers to the abundance of their food), to multifactor 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).

Aggregative models

Aggregative models are based on relationships between forager abundance and food density (the ‘aggregative response’). Relatively few aggregative responses have been measured for vertebrates. For birds, the majority of examples are for various species of waterfowl, seabirds and raptors (Newton 1998). A smaller number of aggregative responses have also been measured for farmland birds (see Fig. 1).

For species that show a clear aggregative response to a certain food type, this approach can provide an indication of how habitat use by this species will respond to changes in the availability of that food. For example, Watkinson et al. (2000) used observational data on the relationship between field use by skylarks Alauda arvensis and weed seed densities within crop fields, to predict how changing seed densities would affect field use by skylarks. Schluter & Repasky (1991) showed that aggregative responses can even be consistent across continents, with broadly similar relationships between
biomass of finches and biomass of seeds in three con-
tinental regions of Africa, North and South America. For
the majority of species, however, four principal draw-
backs restrict the applicability of aggregative models.

First, aggregative responses can be very difficult to
demonstrate empirically. It is often hard to establish
the exact densities of available food and to weight this
according to preference. For example, the distribu-
tion of weed seeds within fields is often extremely
heterogeneous and determining mean densities is, thus,
extremely intensive. To assess the aggregative responses
of skylarks and yellowhammers Emberiza citrinella
to densities of arable weed seeds, Robinson & Sutherland
(1997) determined seed densities by sampling between
10 and 170 locations in each field, depending on field
size. More recent work that has failed to replicate these
findings (Hart et al. 2002), used only two sampling
points per field. Sampling approaches notwith-
sanding, there may be many other factors that influence the
choice of where to forage, in addition to the density of
available food. These may include accessibility (e.g.
Sutherland & Allport 1994) or visibility (e.g. Whittingham
& Markland 2002) of the food, and the avoidance of
predators (e.g. Barnard 1980), interference (e.g. Goss-
Custard et al. 2001) or disturbance (e.g. Gill 1996).

Second, aggregative responses can be misleading
in terms of direct responses to food availability. For
example, Rowcliffe, Watkinson & Sutherland (1998)
reported that dark-bellied brent geese Branta bernicla
bernicla on high salt marsh showed an aggregative
response to the abundance of sea lavender Limonium
vulgare in both winter and spring. However, dietary
and community composition analyses revealed that
L. vulgare is not eaten by the geese, implying that the selec-
tion of feeding sites where it is abundant must be seen
as a preference for the particular community type
dominated by L. vulgare rather than a true aggregative
response. Preferences for a particular community type
may often be more important than preferences for
areas with an abundance of a given food type. Such
preferences may be reflected, for example, by indices
like the habitat suitability index used by Green & Stowe
(1993) to explain habitat selection in corncrakes. How-
ever, these indices do not consider food availability
explicitly and, hence, are not appropriate for predicting
changes in abundance in relation to food supply.
Third, if food is heterogeneously distributed, the scale at which aggregative responses are measured may have important implications for any conclusions drawn from models based on them. Aggregative responses may be linear, showing a direct association with the amount of available prey; concave, indicating a tendency towards conspecific attraction; or convex, indicating the likelihood of some form of conspecific interference. Figure 2 shows that, in heterogeneous environments, predictions regarding the consequences of changing food supply will be sensitive to the shape of the aggregative response and the scale of resolution at which the abundance of food is measured. Only where a population shows neither conspecific attraction nor avoidance, and aggregative responses are linear, will predictions based on mean food abundance be robust to the resolution of measurement.

Finally, and perhaps most importantly, aggregative models tell us nothing about demographic rates and their dependence, or otherwise, on population density. Thus, 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. If high density patches of food exist, foragers may occur only rarely in patches with lower food densities. If the high density patches are removed, however, the foragers may respond by aggregating in much higher densities in areas where food is less abundant. The consequences of this for food intake and population regulation are not predictable on the basis of aggregative models.

**POPULATION MODELS**

The vast majority of published, species-specific population models are phenomenological models, and are based on empirically determined rates of fecundity, mortality and, in some cases, dispersal. To have utility for predicting the consequences of changing food supply, however, models need to link demographic rates explicitly to the availability of food. There are far fewer examples of phenomenological models that fulfil this criterion. For birds, 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).

Pennycuick (1969) used data from an 18-year study of great tits in Oxford, to show that survival of nestlings, juveniles and all individuals over winter were dependent (amongst other factors) on the availability of food (beech mast crop, using an arbitrary scale of abundance). A matrix model was then used to assess the importance of different factors affecting the population size, indicating the overriding importance of density dependent juvenile survival in regulating the population, and of food availability in causing fluctuations around the mean population size.

Potts & Aebischer (1991; references therein) used data from an ongoing study of grey partridges in a relatively closed population inhabiting five farms in Sussex. They showed that in this species, chick survival was heavily dependent on the density of available insect prey, and could be predicted using a weighted index of abundance based on just five main groups. Furthermore, the abundance of these invertebrates depended on the use of herbicides and insecticides; leaving
cereal headlands unsprayed almost doubled the chick survival rate. Nesting limitation due to hedgerow availability, density-dependent nest predation, and density-dependent losses due to shooting and over-winter mortality were also shown to occur. All of these factors were incorporated into a population model, permitting evaluation of the relative efficacy of different management strategies (predator control, unsprayed conservation headlands, and hedgerow replanting).

LIMITATIONS OF PHENOMENOLOGICAL POPULATION MODELS

The approaches used by Pennycuick (1969) and Potts & Aebischer (1991) have proved enormously informative, allowing detailed explanation of past trends and some prediction of future patterns. 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 application of such approaches to a range of other species is limited by several factors. First, as previously observed, the model of the Oxford great tit population drew on 18 years of data. The grey partridge model was based on 21 years of data, with the additional benefit of information from field surveys dating back to the early 1900s. Clearly, studies of few other species provide such a wealth of data that vital rates and their relationships with food can be determined so accurately.

To develop these models for other species of birds, data linking demographic parameters quantitatively to food availability are required. Relationships between food supply and demography have been extensively reviewed by Newton (1998). Although studies linking food supply to demographic parameters are not uncommon for raptors, for farmland birds there are very few published examples of such work. Those that do exist indicate the importance of food for various aspects of demography, e.g. nesting body condition (corn bunting *Miliaria calandra*, Brickle 1998), and fecundity (linnets *Carduelis cannabina*; Moorcroft 2000). Unfortunately, without corresponding information linking, for example, body condition with survival, and reproductive success or nesting survival with density-dependent overwinter mortality, none of these relationships permit the development of a full model linking population dynamics to food supply.

Perhaps the most serious limitation of phenomenological population models is that they can only be applied with confidence within the range of conditions that was used for their parameterization (Bradbury et al. 2001; Norris & Stillman 2002). For example, Newton (1998) summarized 26 studies of the effect of supplementary winter feeding on the breeding density of bird species. Fifteen of these studies showed an increase in breeding densities as a result of supplementary winter feeding. However, 11 studies – including several conducted on species that showed a positive response to supplementary winter feeding in other areas – showed no response to additional winter feeding. Clearly, a model parameterized in an area or under conditions where food was not limiting would not necessarily be useful if food availability were greatly reduced in that area, or if the type of available food were to change.

Behavioural models

At their core, behavioural models are based on the assumption that, to a useful approximation, individuals will behave in a way that maximizes their own fitness (Sutherland 1996). This assumption has great flexibility for predictions in novel environments, as it is unaffected by changes in the environment. Populations may be simulated as a collection of individuals all behaving in a way that maximizes their own fitness. In this way, it is possible to gain a good indication of the spatial distribution and foraging efficiency at the scale of the population. In contrast to phenomenological population models, behavioural models need make no assumptions about the responses of demography to changes in environment, as these responses may be emergent features of the models. A number of different approaches to behavioural modelling exist, however, and the technique is not without problems for making long-term, quantitative population predictions. In particular, Norris & Stillman (2002) drew attention to the fact that behavioural modelling of bird populations has, hitherto, largely been developed to make predictions regarding the non-breeding season. Furthermore, the simpler behavioural models give indications only of how many forager-days an area of habitat can support, giving little indication of the expected population size from year to year. Behavioural models that consider interactions between individuals and their food supply are broadly known as depletion models.

Depletion models are the simplest behavioural models but can vary in several important ways. Typically, the environment is divided into patches of different prey density. The models may be spatially explicit (e.g. Atkinson 1998), or non-spatial (e.g. Gill, Sutherland & Norris 2001). Individual foragers may be modelled explicitly, permitting a range of individual characteristics (e.g. Goss-Custard et al. 1995), or may be modelled using a matrix-type approach (e.g. Sutherland & Allport 1994). Generally, the foragers concentrate in the best patches initially. As the resources in the best patches are depleted, so the range of exploited patches will increase. When all patches have been depleted to a lower critical threshold of food availability – or ‘leaving density’ – then all individuals will leave the habitat. This allows the total number of forager-days in the habitat to be calculated and thus gives an estimate of habitat use but no intimation of demographic performance.

DAILY RATION MODELS

The temporal resolution of depletion models and the methods by which foraging is modelled during each time step may also vary. At one extreme are daily ration models, calculated for the entire period of interest. These require that the total amount of available food (i.e. the total amount of food less the leaving density) is summed across all patches. Knowing the average amount eaten by each forager each day, the total number of forager days that can be supported in the habitat can easily be calculated (e.g. Alonso, Alonso & Bautista 1994). Daily requirements and maximum daily intake rates may be predicted for a wide range of species, using well established allometric relationships. For example, Nagy (1987) reviewed field metabolic rates (FMR, the typical daily expenditure of energy under field conditions) of 25 species of birds, all of which had been assessed using doubly labelled water analyses. He showed that body mass ($M$, in grams) explained over 90% of the variation in FMR and that these factors were related by the equation:

$$\log(FMR) = 1.037 + 0.640 \log(M)$$  \hspace{1cm} \text{eqn 1}$$

Goss-Custard et al. (2003) have shown that for a broad range of conditions, daily ration approaches will give the same predictions as many more complex depletion models. One obvious exception to this is where renewal of resources or losses due to causes other than depletion occur in a temporally stochastic manner. This is expected to occur in farmland, for example, where changes in seed availability due to recultivation of fields or seed production by different weed species may not be regularly predictable events. To overcome this problem, daily ration models may be broken down into smaller time steps, during which each forager eats only an appropriate fraction of its average daily intake (e.g. Sutherland & Allport 1994).

FUNCTIONAL RESPONSE MODELS

A more elaborate approach to modelling foraging is to use the functional response of the forager. The functional response is the relationship between forager intake rate and food density (Solomon 1949). Functional responses may be determined by observing how intake rate varies in patches of naturally varying resource density, or by experimental provisioning with different densities of resource. A variety of functions may then be fitted to these data. Most functional responses are of the 'Type II' form (Hassell, Lawton & Beddington 1976) which is described by Holling's (1959) disc equation:

$$N = \frac{a'\alpha}{1 + a'\alpha T_h}$$  \hspace{1cm} \text{eqn 2}$$

where $N$ is the intake rate, or number of food items eaten per second, $a'$ is the search efficiency of the forager (i.e. the effective area searched with complete efficiency each second), $\alpha$ is the resource density, and $T_h$ is the time taken to handle each food item. Data on intake rates and resource density are available for a small number of granivorous bird species, and analyses using eqn 2 are summarized in Table 1.

The data presented in Table 1 suggest that functional response data for granivores need to be treated with considerable caution. Although debate surrounds the estimation of parameters for the functional response (e.g. Fan & Petitt 1994, 1997; Williams & Juliano 1996), alternative forms of analysis would be unlikely to alter the order of magnitude of the estimates of handling time and search efficiency presented in Table 1. Whilst estimates of the handling time of granivores are consistently in the order of a few seconds, there is much greater variation in estimates of the search efficiency, with estimates spanning three orders of magnitude. Error in estimates of the search efficiency will be particularly critical in affecting predicted forager intake

### Table 1. Functional responses measured for granivorous bird species

<table>
<thead>
<tr>
<th>Bird species</th>
<th>Food source</th>
<th>Experiment (E)</th>
<th>Handling time ($T_h$/s)</th>
<th>Search efficiency ($a'$)/m$^2$ s$^{-1}$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canary</td>
<td>Mixed canary seed on grass</td>
<td>E</td>
<td>5-4</td>
<td>0.0144</td>
<td>Whittingham &amp; Markland (2002)*</td>
</tr>
<tr>
<td>Canary</td>
<td>Mixed canary seed on bare earth</td>
<td>E</td>
<td>4-1</td>
<td>0.0321</td>
<td>Whittingham &amp; Markland (2002)*</td>
</tr>
<tr>
<td>Corn bunting</td>
<td>Wheat (Triticum sp.) grain</td>
<td>E</td>
<td>2-0</td>
<td>0.0007</td>
<td>Robinson (1997)</td>
</tr>
<tr>
<td>Skylark</td>
<td>Wheat grain</td>
<td>E</td>
<td>6-9</td>
<td>0.0062</td>
<td>Robinson (1997)</td>
</tr>
<tr>
<td>Skylark</td>
<td>Various weed seeds of mass &gt; 1 mg</td>
<td>O</td>
<td>10-4</td>
<td>0.0491</td>
<td>Green (1989)*</td>
</tr>
<tr>
<td>Twite</td>
<td>Seeds of Salicornia sp.</td>
<td>O</td>
<td>3-2</td>
<td>0.0024</td>
<td>Atkinson (1998)*</td>
</tr>
<tr>
<td>Woodpigeon</td>
<td>Cereal grain</td>
<td>O</td>
<td>1-3</td>
<td>0.0135</td>
<td>Murton, Westwood &amp; Isaacson (1964)*</td>
</tr>
<tr>
<td>Yellowhammer</td>
<td>Wheat grain</td>
<td>E</td>
<td>3-3</td>
<td>0.0120</td>
<td>Robinson (1997)</td>
</tr>
<tr>
<td>Yellowhammer</td>
<td>Wheat grain</td>
<td>E</td>
<td>5-4</td>
<td>0.0014</td>
<td>Robinson (1997)</td>
</tr>
</tbody>
</table>

*Data reanalysed from source.
rates when resource densities are low. In particular, the differences in estimates of this parameter for single species (skylark and yellowhammer) suggest that functional responses cannot currently be used to model foraging by granivores with confidence.

**PARAMETER ESTIMATION FOR DEPLETION MODELS**

Given the low number of measured functional responses for granivores and the high variability in their parameters, it may appear preferable to use daily ration approaches for these species. If the critical density \(d_c\) is estimated accurately in daily ration models, then these will give identical results for resource densities above this point. Feeding below \(d_c\) is assumed to be negligible and, hence, if \(d_c\) is estimated accurately, daily ration models with an appropriate temporal resolution will be as good as functional response models. However, this raises the questions, how can \(d_c\) be estimated and what would be the consequences of error in the estimate?

The critical density can be estimated from either the aggregative response or the functional response. For the latter method, eqn 2 may be rearranged. \(d_c = \alpha\) when \(N = R/T_{\text{max}}\), where \(R\) is the number of food items required daily (calculated, for example, from eqn 1), and \(T_{\text{max}}\) is the maximum period of time (in s) spent foraging. Thus,

\[
d_c = \frac{R}{a'T_{\text{max}} - a'T_hR}
\]

**eqn 3**

It is possible to assess the consequences of error in the parameters of the functional response, for estimates of \(d_c\) obtained by this method. A simple way of doing this is to assess the effect of proportional changes in estimated parameters on model predictions. This is done by looking at how the predictions of the model vary with each parameter, on a double logarithmic scale (Fig. 3). In fact the results of this are readily summarized by a simple analytical approach, in which the logarithm of \(d_c\) is differentiated with respect to the logarithm of each of the two parameters.

\[
\frac{\partial \log d_c}{\partial \log a'} = -1
\]

**eqn 4**

\[
\frac{\partial \log d_c}{\partial \log T_h} = \frac{T_hR}{T_{\text{in}} - T_hR}
\]

**eqn 5**

Equation 4 shows that an order of magnitude error in \(a'\) will lead to an order of magnitude error in \(d_c\). For error in estimates of \(T_h\), the situation appears more complex (eqn 5). Over a broad range of conditions, estimates of \(d_c\) are relatively insensitive to errors in estimates of the handling time because \(d_c\) generally declines at the same rate as handling time increases. The exception to this is when the estimated handling time approaches the limit at which it alone would be sufficient to prevent the forager from achieving its required daily intake. Where this is the case, it is likely that the functional response has been measured incorrectly and the data should not be used for modelling foraging. The results of this for the relative accuracy of daily ration and functional response models are shown in Fig. 4. Clearly, above the estimated critical density, the results of both types of model are prone to similar errors. Below this density, functional response models are the more accurate, as they do permit some foraging (and therefore, the acquisition of some proportion of the daily requirement), whereas daily ration approaches permit no foraging at
all. However, below the critical threshold, foraging is negligible and, thus, the predictions of the two modelling approaches and their sensitivity to error, are basically the same.

INTERFERENCE

Interference is a reversible process by which intake rates are affected by the density of foragers within a patch. It may affect the time budgets and distribution of foragers and can be incorporated into depletion models when foraging and intake rate are explicitly included in the model (using the functional response). Increased interference at higher forager densities may be caused by a variety of mechanisms (Goss-Custard 1980), including disturbance, increased aggression, and increases in the frequency of food theft (kleptoparasitism). Disturbance can result where high forager densities lead to food becoming trampled, or prey species moving to less accessible areas. This is likely to be less serious when feeding on non-motile prey (Goss-Custard 1970). Aggression is more common in territorial species and, for many species therefore, is likely to be more important in the breeding season. Kleptoparasitism has been shown to be less frequent when foragers feed on a relatively low value resource that can be quickly swallowed (Sutherland & Koene 1982). For many species, it has been suggested that interference may be less important than individual foraging efficiency (Caldow et al. 1999; Stillman et al. 2000a).

For farmland birds and analogous granivores, evidence regarding the importance of interference is equivocal. Interference has been demonstrated in some granivorous passerines (e.g. Dolman 1995; Johnson, Girardeau & Grant 2001). However, broad reviews of the evidence indicate that, amongst all bird species, the
most common relationship between food intake and group size is a monotonic increase; furthermore, this pattern was most commonly associated with birds feeding on seeds (Beauchamp 1998). A common explanation for this phenomenon is the reduction in individual vigilance that arises in larger groups of birds (e.g. Jennings & Evans 1980). The benefits of reduced anti-predator vigilance may be outweighed by increases in vigilance directed at competitors (Cresswell 1997) but no evidence that this component of vigilance behaviour increases in larger groups was found for granivores (Lima, Zollner & Bednekoff 1999). Interference may also affect individuals in different ways (Cresswell 1998a; Smith, Ruxton & Cresswell 2001), although this effect may not be consistent across habitats (Cresswell, Smith & Ruxton 2001). Finally, it is not yet clear whether interference is independent of resource density (Beddington 1975), or is higher at low (Dolman 1995) or intermediate resource densities (Cresswell 1998b). Overall, interference remains poorly understood in farmland birds but the widespread occurrence of flocking among farmland passerines and thrushes, suggests that the benefits of conspecific attraction outweigh the costs of interference. Where interference is important, it may affect time budgets and lead to trade-offs between predation risk and intake rate (Beauchamp & Livoreil 1997). Including these effects in models would require complex simulations of time budgets, energetics and predation risk, and could only be incorporated in functional response models. Given current uncertainty regarding functional responses for granivores, it is unlikely that this would be possible at present.

RECOMMENDATIONS FOR DEPLETION MODELLING OF GRANIVOROUS BIRDS

From the above sections, we conclude that currently, daily ration approaches are likely to be as useful as functional response approaches for modelling. Functional response models permit a greater range of factors and behaviours to be incorporated but, at present, many of these (such as interference) are poorly understood for farmland birds. The greater range of potential behaviours that can be incorporated in functional response models permits greater scope for behavioural verisimilitude but this has costs, including an increase in the requirements for data, and sensitivity of predictions to an increased number of parameters. At their most basic, daily ration approaches permit sensitivity analyses to be carried out on a single parameter ($d_1$), rather than two parameters ($T_b$ and $a$, the effects of which are summarized by their effect on $d_1$). The critical density may be varied through realistic ranges of values calculated both by using eqn 3, above, and also derived from aggregative responses. Critical densities may be derived from aggregative responses by assuming that the critical density is approximately equal to the lowest density at which birds were observed to feed. These are unlikely to be accurate but will give some indication of the correct order of magnitude. Using the functional responses listed in Table 1 and aggregative responses shown in Fig. 1, critical densities are estimated to lie somewhere between 0.5 and 12.5 kJ m$^{-2}$, with a modal estimate in the region of 5 kJ m$^{-2}$.

PREDICTIONS OF BEHAVIOURAL MODELS

An important requirement of behavioural models is that the dynamics of the resource populations are well understood. This means that behavioural models will often be most easily applied to highly specialized foragers that feed on only one or a few types of prey, with the most reliable results being produced for seasons in which rates of resource renewal are closest to zero. For the majority of farmland birds that feed on a wide variety of invertebrate and plant species during the breeding season, modelling interactions with their resources during this period is likely to prove highly complex. Behavioural population models that also consider the breeding season, rarely include an explicit treatment of foraging during this season (e.g. Stillman et al. 2001). Rather, population dynamics in the breeding season are modelled using phenomenological data on fecundities. As already observed, relationships between fecundity and resource availability for farmland birds are sparse, and this approach would be restricted to species such as the grey partridge. Furthermore, behavioural foraging models usually predict the point at which foragers will either die, or will leave an area to forage elsewhere. In order to incorporate these into full population models, it is necessary either to assume a closed population (an unrealistic assumption for many species), or to have an understanding of the fate of individuals that do leave to forage elsewhere. Therefore, despite the obvious appeal of full population models, for the majority of species these will be no more informative than models that consider only numbers of foragers that can be supported during the non-breeding season.

Two types of prediction may be made using models of dynamics during the non-breeding season. First, as previously discussed, it is possible to estimate the number of forager-days that an area of habitat can support over winter. In a system that can support 100 forager days over winter, the forager-days approach makes no distinction between 100 foragers removing their daily requirement on day 1 of the model, and one forager removing its daily requirement each day for 100 days. Where there is feedback between the foragers and their resource, the level and temporal distribution of depletion may have serious consequences for the resource dynamics. Arable weed communities are such systems and the forager-days approach would be inappropriate in these cases.

The second type of prediction that may be made is an estimate of the likely population size at the end of winter. This is possible using either an energetic flux approach, an individual-based approach with individual
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variation, spatial constraints or decision error, or an iterative approach. The energetic flux approach combines estimates of rates of uptake, storage and expenditure of energy, in order to model individual energy reserves and to predict the point at which an individual will die. This approach has been pioneered by Stillman et al. (2000b), who noted that their model (constructed for oystercatchers Haematopus ostralegus feeding on mussels Mytilus edulis) was particularly sensitive to energetic parameters, including estimates of energy expenditure and assimilation as reserves. At present, these parameters are not known with such accuracy for the majority of farmland birds as for the well-studied oystercatcher. Given that many such species are of conservation concern, further research on their energetics may well be beneficial.

It is difficult to predict mortality using standard depletion models. In a uniform environment models will predict that all foragers will feed equally until available resources are completely depleted, at which point all the foragers will either leave or die together. Instances of mass-mortality have been documented amongst (mostly marine) birds (e.g. Piatt & Van Pelt 1997; Baduini et al. 2001; Camphuysen et al. 2002) and may occur at a localized scale amongst farmland birds. However, such events are likely to be rare, begging the question, what does lead to more gradual mortality rates in reality? Putative mechanisms include individual differences in requirements, error, or spatial constraints. Assigning birds a body mass drawn from a random distribution of plausible masses, means that different individuals will have different daily requirements. However, except in a system with high rates of resource inputs, variation in body mass would have to be implausibly high in order to stagger deaths over more than a few days. Similarly, only large variations in foraging efficiency (reflected, for example, in different critical thresholds for different individuals), would lead to mortalities being staggered over an entire season. Decision error (owing to individuals having an incomplete knowledge of the best feeding locations), travel costs and sampling restrictions may all contribute to deviations from ideal free behaviour and, thus, uneven patterns of mortality. However, all are currently difficult to introduce into depletion models. Decision error would introduce a further unmeasurable assumption, whilst the other approaches are also hard to measure for the majority of farmland birds and would require a spatially explicit modelling framework. A spatially explicit model would, in turn, require that resource availability could also be modelled at a spatial resolution appropriate for the heterogeneity of its distribution. The principal food resource of many farmland birds in the non-breeding season is weed seeds, which may be extremely heterogeneous in their distribution, even at the scale of individual weed plants. However, models currently available to simulate weed dynamics (e.g. Freckleton & Watkinson 1998; Lintell Smith et al. 1999) are deterministic, based on mean seed and plant densities over an area. Thus, efforts to incorporate variation in individual fates through these methods may require a new approach to modelling resources at a far finer spatial resolution.

Perhaps the easiest way to determine sustainable populations over winter, is by using an iterative approach (Atkinson 1998). This approach involves recording the state of the environment (including the availability of all resources) at the start of the non-breeding season and then iteratively sending populations through winter. If the population survives, then it is reasonable to take this as the population size that emerges in the spring. If, however, the population does not survive, then it is reasonable to assume that the population at the end of winter would be smaller than that being tested. In this case, start conditions can be reinstated and a smaller population (reduced, for example, by 5%) sent through winter. In this way, it is possible to determine (within the limits of the stochastic nature of the model environment) the largest population that can survive the whole winter. Thus, the iterative approach allows predictions of the most positive population consequences possible under any scenario, a strong indication of the value of the habitat and of the consequences of a change in that value. Importantly, this approach allows the maximum population emerging in spring to be predicted and, thus, can be used in conjunction with demographic models of the breeding season.

Conclusions

PREDICTIVE MODELS FOR GRANIVOROUS BIRDS

The techniques available for predicting the response of farmland bird populations to changing food supplies are summarized in Table 2. In terms of the types of predictions possible, as well as applicability to novel circumstances, it is clear that functional response models have the highest potential of the four approaches discussed. However, due to the current unreliability of data on functional responses of granivores we suggest that, at present, daily ration approaches have the greatest utility of those discussed. Given current constraints on available data, long-term population forecasting will be most feasible using a model that predicts over-winter populations using an iterative daily ration model but a phenomenological model of breeding season dynamics based on empirical data. The iterative approach will allow the maximum number of birds emerging at the end of winter to be predicted. The phenomenological approach will allow the number of birds entering the following winter to be predicted. Thus, the two approaches will combine to predict future trends in the maximum number of birds supportable by the habitat. The phenomenological approach should link breeding dynamics to resource availability wherever possible.
The credibility of simulation models of the effects of environmental change will be greatly enhanced by widespread model validations. A variety of methods are available for the validation of phenomenological models. By contrast, behavioural models are much harder to validate, especially when their predictions are on a very large temporal and spatial scale. We suggest that two methods could be employed to increase confidence in such models. First, models can be tested on a small scale by generating predictions for experimental set-ups. Validation of predictions even at the scale possible within an aviary will both contribute to confidence in models and aid in their development. Within a larger time-frame, validations may take advantage of the large number of agri-environment schemes adopted in Europe. Many such schemes aimed at enhancing biodiversity have been implemented but the majority are subject to limited and poorly designed monitoring. It has been suggested that monitoring should be an integral part of future schemes (Kleijn & Sutherland 2003). Model-based predictions of the effects of such schemes would provide a useful tool for assessing competing methods and allocating funds, whilst the outcome of the schemes would aid model validation.

### Limitations of Available Data and Directions for Further Work

Available data severely limit the range of approaches for predicting the response of farmland bird populations to changing food supply. These limitations apply both to phenomenological models and to behavioural models. In particular, further research in four main areas is desirable to enhance the power of predictive models.

#### Aggregative Responses

As discussed previously, aggregative responses are surprisingly time-consuming and difficult to collect. Nevertheless, they represent one of the most straightforward tools available to modellers for predicting the consequences of changing food availability. At present, very few examples of aggregative responses for farmland birds are available from published literature. Collecting aggregative responses for more farmland birds should be a priority, not only to aid the resolution of problems with these relationships, but also to provide more information on the distribution and abundance of resources for farmland birds.

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**Table 2. Summary of major modelling approaches intended to relate farmland birds to their food supply**

<table>
<thead>
<tr>
<th>Model approach</th>
<th>Includes individual variation</th>
<th>Incorporates depletion of resources</th>
<th>Ease of model construction and parameterization</th>
<th>Type of predictions</th>
<th>Drawbacks of the approach</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Phenomenological models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aggregative responses</td>
<td>N</td>
<td>N</td>
<td>Models are simple to construct and can be based on as little as a single season’s fieldwork on bird distributions in relation to resources</td>
<td>Field use in relation to resource density but no demographic rates</td>
<td>Underlying data may be hard to establish, difficult to replicate and highly context dependent. Permit only limited inferences about the fate of populations</td>
</tr>
<tr>
<td>Population models</td>
<td>Y/N</td>
<td>N</td>
<td>Models are simple to construct but usually require many years of fieldwork to parameterize</td>
<td>Demographic rates and population performance in relation to resource density</td>
<td>Extremely difficult to parameterize and only applicable under the conditions that prevailed during their parameterization</td>
</tr>
</tbody>
</table>

**Behavioural models**

| Daily ration models      | Y/N                           | Y                                 | Models can vary greatly in their complexity but are rarely as simple to construct as phenomenological models. They can be parameterized from well-established relationships between body mass and energetic requirements, although establishing critical densities for economic foraging may take weeks or months | A range of possible predictions, depending on model structure, from forager-days that a resource can support, to total carrying capacity over a season | Do not predict demographic rates, so mortality can only be inferred from carrying capacity |

| Functional response models | Y/N                           | Y/N                               | May also vary in their complexity. Although considerable effort has been expended on determining functional responses for granivores, these need to be determined with a high degree of accuracy and over a broad range of conditions. Thus, models may take many months or years to parameterize | A range of possible predictions, depending on model structure, from forager-days that a resource can support, to individual condition and demographic rates | Functional responses for granivores cannot currently be treated with confidence and, given the range of factors that may confound their accurate measurement, may not be for some time |
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Food supply and demography

A crucial limitation of both phenomenological population models and the breeding season component of behavioural models is the lack of data linking demography to food supply for granivorous birds. Many autecological studies of farmland passerines produce excellent data on the reproduction and survival of these species. However, measuring food supply should also be standard practice within such studies, in order that the critical link between food availability and both summer and winter density dependence may be better understood. Density dependence is unlikely to be easily inferred from studies of only a few years’ duration and, consequently, long-term studies, such as that of the grey partridge, remain of very high value.

Critical food densities and functional responses

The estimation of food densities below which foragers cannot obtain their required daily intake is important for depletion models, regardless of the mechanism used to model foraging. Approximate values for critical densities can be determined from aggregative responses and this provides a further reason for increasing the number of aggregative responses available for farmland birds. Critical densities may also be derived from functional responses. More studies, both in the field and in aviaries, are needed to determine functional responses more accurately, and for a greater number of granivorous species. Given the tight allometric relationships between body mass and energetic requirements, it might also be expected that functional responses would show similar scaling rules for species with similar diets. For example, small seeds may be hard to find (high $T_a$) but very quick to eat (low $T_b$), whereas large seeds are likely to be easy to find (low $T_a$) but take longer to deal with (high $T_b$). Considerably more functional responses are required if such generalities are to be determined and to increase the speed with which behavioural models can be constructed.

Breeding season diet and relation of demography to food dynamics

The year-round dynamics of many arable weeds and their seed production are reasonably well understood. However, during the breeding season, many farmland bird species adopt a much broader and more flexible diet, including a wide variety of seeds, plant matter and invertebrates. We have already alluded to the dearth of studies linking demography to food availability in summer. For behavioural models of foraging during this period it is also necessary to understand spatio-temporal patterns of the abundance and depletion of resources. This, in turn, demands detailed studies of diet, foraging ecology and resource availability for farmland birds during the breeding season.

References


In conclusion, simulation modelling techniques available for predicting the consequences of changing food supply for farmland birds, have largely outstripped the availability of data required to parameterize them. Detailed predictions are possible only for a limited number of species in a restricted set of circumstances. Current simulations should rely most heavily on daily ration modelling, as this approach has the greatest generality and requires the least specific inputs. Concurrent efforts should be focused on gathering species-specific data on a greater range of species, such that more general rules can be discerned from species-specific approaches.

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