Evidence for the indirect effects of pesticides on farmland birds

NIGEL D. BOATMAN,^{1*} NICHOLAS W. BRICKLE,^{2,3} JUSTIN D. HART,¹ TIM P. MILSOM,¹ ANTONY J. MORRIS,⁴ ALISTAIR W. A. MURRAY,¹ KATHRYN A. MURRAY^{5,6} & PETER A. ROBERTSON¹ ¹Central Science Laboratory, Sand Hutton, York YO41 1LZ, UK ²School of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK ³The Game Conservancy Trust, Fordingbridge, Hampshire SP6 1EF, UK ⁴The Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, UK ⁵Allerton Research and Educational Trust, Loddington, Leicestershire LE7 9XE, UK ⁶Harper Adams University College, Newport, Shropshire TF10 8NB, UK

Indirect effects of pesticides, operating through the food chain, have been proposed as a possible causal factor in the decline of farmland bird species. To demonstrate such a link, evidence is needed of (1) an effect of food abundance on breeding performance or survival; (2) an effect of breeding performance or survival on population change; and (3) pesticide effects on food resources, sufficient to reduce breeding performance or survival, and hence to affect the rate of population change. Evidence under all three categories is only available for one species, the Grey Partridge Perdix, although data showing effects of pesticides on food resources and relationships between food resources and breeding performance are also available for some other species. This paper reports on recent work investigating the effects of pesticides on Yellowhammer Emberiza citrinella and Skylark Alauda arvensis during the breeding season. The probability of brood reduction in Yellowhammer was affected by the proportion of the foraging area around the nest which was sprayed with insecticide. No significant effects of pesticides were recorded on Skylark chick condition or growth rate, but sample sizes were small. Invertebrate food abundance affected chick condition (Skylark) and the number of chicks fledging (Yellowhammer and Corn Bunting Miliaria calandra; relationship for the latter derived from re-analysis of data from an earlier study). Other recent work is briefly reviewed and the current evidence for the indirect effects of pesticides is summarized. Significant knowledge gaps are identified and some of the issues involved in resolving these are discussed.

Over the last three decades, substantial declines have occurred in the range and abundance of a number of farmland bird species, which have been linked to the intensification of agriculture (Chamberlain *et al.* 2000, Donald *et al.* 2001a, Newton 2004). Potential mechanisms are reviewed by Fuller (2000), and include the effects of pesticides.

Concern about the effects of pesticides on birds in the UK was first stimulated by the effects of organochlorine insecticides in the 1950s and 1960s (Newton 1995). Since the withdrawal of these pesticides, populations of affected bird species have largely re-

*Corresponding author. Email: n.boatman@csl.gov.uk covered, and there is now little evidence of significant population effects arising from direct effects of pesticides in the UK, with the possible exception of the potential impacts of new generation rodenticides on predatory bird species such as the Barn Owl *Tyto alba* and the Red Kite *Milvus milvus* (Burn 2000).

Although direct effects of pesticides are now less evident than previously, there is still concern about the potential indirect effects of pesticides, operating through the food chain. Impacts of pesticides on weeds and invertebrates may reduce the availability of food resources, affecting productivity and/or adult survival. Three main mechanisms have been identified through which pesticides may affect food availability for birds: (1) insecticides may deplete or eliminate arthropod food supplies, which are exploited by adults and their dependent young during the breeding season and, in so doing, reduce breeding productivity;

(2) herbicides may reduce the abundance of, or eliminate, non-crop plants that are hosts for arthropods taken as food by farmland birds during the breeding season, and thereby reduce breeding productivity;

(3) herbicides may also deplete or eliminate weed species, which provide either green matter or seeds for herbivorous and granivorous species, respectively, thereby reducing survival of those birds that rely on those food supplies.

The effects of pesticides on arthropods important in chick diet were identified as a major causal factor in the decline of the Grey Partridge *Perdix perdix*, and this species provides the best documented case study of such effects (Potts 1986). Campbell *et al.* (1997) reviewed the evidence for the role of indirect effects of pesticides on farmland birds, and concluded that there were possible effects on at least 11 further species, though only for Grey Partridge had such effects been conclusively demonstrated.

In order to test the hypothesis that indirect effects of pesticides are a significant causal factor in declines of bird species, it is necessary to test the existence of relationships at a number of levels within a causal framework or conceptual model. The three key steps in this conceptual model are:

(1) evidence of a relationship between food abundance/availability and breeding performance or survival;

(2) evidence of a relationship between breeding performance or survival and population change;

(3) evidence of pesticide effects on abundance and/ or availability of bird food resources, sufficient to reduce breeding performance or survival, and hence to affect the rate of population change.

Evidence of pesticide effects on food resources and relationships between food resources and breeding performance can be obtained through autecological or experimental studies. Apart from research on the Grey Partridge, reviewed by Campbell *et al.* (1997), such studies have been carried out for Red-legged Partridge *Alectoris rufa* (Green 1984), Pheasant *Phasianus colchicus* (Hill 1985), Corn Bunting *Miliaria calandra* (Brickle *et al.* 2000) and Yellowhammer *Emberiza citrinella* (Morris *et al.* 2002, 2004).

Hill (1985) found a positive relationship between chick survival and insect densities, which accounted for 75% of the variation in chick survival rate. However, Green (1984) found that the diet of Red-legged Partridge chicks was dominated by seeds, leaves and flowers, and they were less dependent upon invertebrates than Grey Partridge and Pheasant chicks. Neither of these studies tested effects of pesticides. Brickle et al. (2000) found that both chick weight and nest survival at the nestling stage for Corn Bunting were negatively correlated with invertebrate food availability, and chick food items were more abundant in foraging areas than in non-foraging areas. Chick food abundance was negatively correlated with number of insecticide applications to cereal fields, although relationships with herbicide and fungicide use were non-significant. However, when all foraging habitats were considered, chick food abundance was significantly negatively correlated with numbers of applications of insecticides, fungicides and herbicides. Furthermore, fields in which Corn Buntings foraged received fewer applications of herbicide, fungicide and insecticide on average than fields which were not used.

Morris *et al.* (2002, 2004) found that three measures of invertebrate numbers ('all' invertebrates, 'important' invertebrates and invertebrates ≥ 5 mm) and biomass were all significantly lower in fields treated with insecticide during the summer than in fields with no or winter-only insecticide applications. There was weaker and less consistent evidence for effects of fungicides and herbicides.

Yellowhammer nestling diet on British arable farmland includes cultivated cereal grain, once it becomes semi-ripe. For earlier nests, where foraging took place before grain was available, foraging density (Morris *et al.* 2001) in fields that received no summer applications of insecticide was nearly four times higher than in fields with summer applications. However, for later nests where grain was available, insecticides did not significantly affect foraging patterns.

Chick condition was related to number of insecticide applications. There was a weak positive relationship between mean brood condition and number of applications up to one application, and a strong negative relationship with more than one application. However, no relationships were detected between pesticide use and chick survival in this study.

Further evidence of pesticide effects on food resources comes from the Game Conservancy Trust's Sussex study. Analysis of long-term monitoring data over an area of 62 km² showed negative relationships between herbicide use and weeds, and also between insecticide use and invertebrates, over a period of 25 years. Effects of summer insecticides on invertebrate numbers were greater than effects of insecticides applied in the autumn, although significant effects of autumn-applied insecticides were detected. Densities of Grey Partridge, Corn Bunting and Skylark were higher where the number of pesticide applications was low (Ewald *et al.* 2002).

Relationships between food abundance and survival are more difficult to demonstrate because of the difficulty in measuring adult survival for most species at a local level, and predictive depletion modelling has therefore been recommended to estimate the potential impacts of variations in food supply, in the absence of direct measurements (Stephens et al. 2003). The establishment of relationships between breeding performance and/or survival and population change relies on the availability of longterm monitoring or survey data. Demographic models of such relationships have been developed for a number of species, based on large-scale survey data (e.g. Siriwardena et al. 1998a, 1998b, 2000), but only for Grey Partridge has a direct relationship between breeding performance and survival of a monitored population been demonstrated (Potts 1986, Potts & Aebischer 1991, 1995).

This paper describes further work carried out since the review of Campbell *et al.* (1997), and summarizes the current evidence for indirect effects of pesticides. Previously unpublished results are presented from autecological work on Skylark *Alauda arvensis*, carried out on commercially farmed study sites, and models are derived relating Corn Bunting and Yellowhammer chick survival to invertebrate food abundance, based on data collected by Brickle *et al.* (2000) and Morris *et al.* 2004). We also present data for Yellowhammer from a designed experiment set up specifically to test the hypothesis that indirect effects can impact on spring settling densities and breeding success.

METHODS

General

For all species, fieldworkers located nests by mapping territorial males and watching for signs of breeding behaviour. If a nest was located at the egg or building stage, brief monitoring visits were made at intervals until it failed (through predation or abandonment) or the eggs hatched. Once a nest contained chicks, a variety of methods were used to obtain data on aspects of chick performance.

Details of pesticides used on study areas were supplied by the farmer or farm manager of the site, from farm records.

Yellowhammer

Autecological studies

Full details of Yellowhammer study sites are given in Morris *et al.* (2004), and details of methodology are given by Morris *et al.* (2002, 2004). Data were collected on pesticide use, invertebrate availability, foraging, chick condition, growth rate and chick survival.

Further analysis was carried out on data from the Royal Society for the Protection of Birds (RSPB) Yellowhammer study to investigate relationships between brood reduction and invertebrate abundance. Invertebrate data from cereal fields were used to calculate means for three different measures of abundance per sample (circle of 50 mm radius; Morris et al. 2004) and biomass. These values were then multiplied by the area of cereal crop within a radius of 200 m of the nest, within which 90% of foraging flights were found to occur. The relationships between three invertebrate food indices and mean brood mass, with tarsus length as a covariate, and the proportion of nestlings that starved in a brood were modelled using generalized linear mixed modelling (GLMM) procedures (Welham 1993), which allow for grouping the data. In this case the data were grouped into farms and 'farm' was treated as a random effect. However, in these models, the predicted values derived from the GLMM were not close approximations to the observed values, so the analyses were repeated as general linear models (GLMs) with farm as a fixed factor (with only three farms in the analysis, treating 'farm' as a fixed factor is acceptable, as GLMMs will not accurately estimate between farm variance; S. Langton pers. comm.).

Designed experiment

A large-scale replicated field experiment was conducted at three sites, in which food resources were manipulated to demonstrate the magnitude of any indirect effects. Sites were located in Hampshire, Lincolnshire and North Yorkshire, on arable or arable/ mixed farms. Crops grown on the study sites included winter wheat, winter and spring barley and oilseed rape (Hampshire), winter wheat, spring barley, sugar beet, peas and linseed (Lincolnshire), and winter wheat, winter barley, oilseed rape, potatoes, spring beans and set-aside (Yorkshire). Treatments in these experiments aimed to enhance winter food availability by providing supplementary seed supplies, and depress invertebrate food resources in summer by increasing insecticide inputs above normal practice. At each site, four treatments were applied: additional insecticide only, supplementary seed only, additional insecticide and supplementary seed, neither (control) giving a factorial design. Each treatment was applied to a 1-km² block of land at each site. Only the effects of insecticide treatments are reported here. Results of supplementary seed provision are reported by Robinson *et al.* (2004).

The aim of the 'additional' insecticide was to apply an extra treatment during the summer, above the normal practice for the farm in question. Data on pesticides applied to study fields were obtained from farm records. The mean (\pm se) number of insecticide applications over all sites was 0.403 \pm 0.079 on blocks with the 'normal' regime, and 1.728 \pm 0.079 on blocks with the elevated insecticide regime.

At each site, baseline data were gathered during the breeding season in the first (non-treatment) year, supplementary seed was applied in the following winter and insecticide manipulations were carried out in the following summer. Entry of sites into the experiment was staggered so that recording and treatments began in successive years, as follows: Hampshire (1999–2000); Lincolnshire (2000–01); Yorkshire (2001–02).

Yellowhammer was selected as the main study species, for three main reasons: (1) chick diet is dominated by arthropods (though later in the season, unripe grain is also consumed) (Wilson et al. 1996, Stoate et al. 1998); (2) it forages in arable crops as well as field margins (Morris et al. 2001, Stoate et al. 1998, J. Hart unpubl. data); (3) it has declined on farmland, although the decline started more recently than that of other farmland species (Gregory et al. 2004). An analysis by the British Trust for Ornithology (BTO) of turning points in smoothed Common Bird Census indices from 1966 to 2000 showed that. on farmland, the decline in Yellowhammer numbers started around 1984 (http://www.bto.org/birdtrends/ wcryelha.htm) yet for all habitats, the onset of the decline occurred 10 years earlier (c. 1974), which was coincident with the onset of the decline in Corn Bunting (http://www.bto.org/birdtrends/wcrcorbu.htm) in 1973-74. One possible explanation is that the causes of the decline in Yellowhammer and Corn Bunting populations on farmland were the same, but that the decline in Yellowhammer populations on farmland was buffered by populations in less preferred habitats, such as woodland (cf. O'Connor 1984), whereas Corn Bunting populations were not.

Recent research in Oxfordshire suggested that Yellowhammer breeding productivity was too low to

© Crown copyright 2004, Ibis, 146 (Suppl. 2), 131-143

maintain a stable population (Bradbury *et al.* 2000), yet it is still sufficiently abundant to provide adequate sample sizes in this type of study.

The effects of the food manipulations were monitored by taking regular samples of seeds and arthropods. Counts of breeding birds were carried out, using a mapping method, over three breeding seasons (pretreatment, treatment and post-treatment) at each farm. Repeated field-by-field counts of all bird species were also performed between November and March.

Data on breeding performance of Yellowhammers were collected in both the pretreatment year and the treatment year. Nests were located by observing adult behaviour and by searching systematically in suitable locations. The progress of each nest was monitored by regular checks every 2-4 days to minimize disturbance. A nest was designated an outcome according to whether the brood was predated, starved, deserted or fledged. Confirmation of fledging was obtained by observing adult warning calls or provisioning behaviour in the vicinity of the nest. Broods were assumed predated if the nest was found empty before the brood had reached a minimum fledging age of 8 days, or there was evidence that the nest had been disturbed. Partial losses of nestlings (brood reduction) were observed from some nests and it was assumed that these losses were due to starvation. If the whole brood perished through repeated partial losses of young the nest was assumed to have starved. If a whole brood was found dead within the nest with no prior evidence of starvation then the brood was assumed to have been deserted.

A GLM (logit link, Bernoulli/binomial errors) was fitted to brood reduction (0/1 binary indicator), using Genstat 5. The model was initially fitted using the treatment factors (i.e. grouping nests by 'normal' and 'extra' spray) to data from sites and years where the spray treatments were applied. This model showed no significant effects of treatment at the block level. Nests were therefore considered on an individual basis. Nests were plotted on a GIS map of the farm, and the proportions of a 200-m-radius area around each nest receiving insecticide spray at different times before hatching were calculated. A non-parametric Kruskal-Wallis one-way analysis of variance showed that only at one site was there a statistically significant difference (P < 0.01) in the proportion of the 200-m-radius foraging area sprayed \leq 20 days from hatching between the sprayed and unsprayed blocks. Data were therefore re-analysed on a nest-by-nest basis, ignoring the block structure and using continuous covariates: proportion of the 200-m-radius foraging area sprayed ≤ 20 days before hatching, and proportion of the 200-m-radius foraging area sprayed > 20 days before hatching. A finer time division was explored but found to be unnecessary.

Two datasets were used for model fitting. Both were restricted to nests in years when extra sprays were planned/applied and the covariate information was available. The first comprised nests from which at least some chicks fledged (n = 64), and the second of nests in which brood reduction was observed (n = 95); the latter included some nests that were later predated or where all the chicks starved.

Skylark

Data from RSPB studies

For Skylark, data from three arable farms in Norfolk and Suffolk and one mixed farm in Berkshire were collected as part of an RSPB study into the species between 1996 and 1999. Details of the study sites are described by Donald *et al.* (2001b, 2002).

Data were collected by the RSPB on pesticide use, chick condition, growth rate and chick survival. Methods of obtaining chick measurements are described by Donald *et al.* (2001b, 2002). Data on nestling condition were available for the analyses presented here from 33 Skylark broods. Data on growth rates (using weight and tarsus length measurements from two successive nest visits) were available from 13 broods. Data on chick survival were available from 43 nests. Pesticide data were collected retrospectively for all arable and non-grass forage crops on the study sites.

Two variables were derived for analysis of Skylark data collected by the RSPB: (1) total number of product applications for herbicides, fungicides and insecticides; and (2) timing of application as a threelevel factor – 'none', 'non-breeding season only' or 'breeding season' (March–early August). The analysis was similar to analysis of the Yellowhammer data (details in Morris *et al.* 2002, 2004), except that an additional variable identifying the field in which the nest was placed was nested within the farm variable, to take account of spatial autocorrelation between nests within the same field. Predated nests were excluded from the analysis.

Data from the Allerton Trust, Loddington

The RSPB Skylark study did not assess the availability of invertebrate food for the chicks, so additional data were collected by Allerton Trust staff from 11 nests at Loddington in 2002 (Murray 2004). Data on chick growth rates and survival were collected as in the RSPB study. Invertebrates were sampled with a Dietrich vacuum sampler (DVac) within a 'core' foraging area defined by a circle of 100 m radius around the nest. Eighty-nine per cent of foraging trips were within this distance of the nest. DVac samples were collected at three random locations from each habitat within this circle. Habitats sampled included winter wheat, winter barley, oilseed rape, winter beans, 'wild bird cover' sown to kale (in first or second year) or wheat plus linseed, beetle banks, grass set-aside, verges and tracks. At each location, two groups of five subsamples were taken within an area of approximately 2 m^2 , each suck lasting for 10 s. These were bulked and frozen in polythene bags before being extracted by hand and stored in alcohol. Invertebrates were identified to order, suborder or (in the case of Coleoptera) family level.

Invertebrate data from different habitats around each Skylark nest at Loddington were weighted according to the extent of the habitat within the sample circle, representing a notional 'foraging area'. Nest locations were plotted on a digitized map of the farm, and the area of each habitat within the circle of 100 m radius around the nest was calculated. using ArcGIS software. Invertebrate numbers sampled from each habitat were then adjusted according to the proportion of the habitat within the foraging circle, before summing the habitats to give a total index of invertebrate availability for each nest. Only those invertebrate groups recorded in the diet of Skylark chicks by Poulsen et al. (1998) were included in the chick food index used in the statistical analysis (Table 1).

The relationships between mean chick mass per nest at days 5–9 and chick food index, and daily growth rate between days 2–6 and chick food index, were examined using linear multiple regression analysis. In order to take account of differences in the ages of chicks between nests, mean tarsus length was also included as a covariate in the analysis of chick mass.

Corn Bunting

Brickle *et al.* (2000) took arthropod samples within a 115-m radius (one-third of the maximum foraging distance observed) for each of a sample of 60 Corn Bunting nests from the South Downs in Sussex, and calculated a food index for each nest. Arthropod abundances for each taxon were weighted to reflect dietary preferences of Corn Buntings. Data were also
 Table 1. Insect groups included in the chick food index for Skylark

 broods recorded at Loddington (derived from Poulsen *et al.* 1998).

Order	Suborder and family		
Ptervgotes			
Hemiptera	Heteroptera		
	Homoptera		
Thysanoptera	·		
Neuroptera			
Coleoptera	Carabidae		
	Staphylinoidea		
	Chrysomeloidea		
	Scarabidae		
	Curculionoidea		
Diptera	Tipulidae		
Lepidoptera			
Hymenoptera	Symphyta (Sawflies) Ichneumonoidea		

collected on pesticide use, invertebrate availability, foraging, chick condition and chick survival. Full details of study sites and methodology are given in Brickle *et al.* (2000).

Brickle *et al.* (2000) found that nest survival at the nestling stage was significantly related to food availability, but did not define the relationship. The relationship between the probability of a Corn Bunting brood surviving to fledging and the Corn Bunting food index was modelled here for 64 nests using data from the Sussex Corn Bunting study, and a binary logistic regression procedure in GLIM4 (Francis *et al.* 1993).

RESULTS

Results will be considered for each species separately. Only the effects of pesticide use in summer are considered here.

Yellowhammer

Autecological studies

The GLMM analysis of the RSPB Yellowhammer data showed no significant relationship between invertebrate abundance or biomass and nestling condition.

However, abundance of invertebrate taxa important in Yellowhammer diet was negatively related to levels of chick starvation (Wald 4.19, P = 0.041, df = 1). Results from GLMs indicate that all three invertebrate number response variables were highly significant predictors of nestling starvation (Table 2). The predicted relationship between Yellowhammer brood reduction and abundance of 'important' invertebrates is shown in Figure 1, along with observed values, grouped using the 'bin' method. Note that the numbers of observations in each bin are quite small owing to the small number of nests in this analysis. The observed values agree reasonably well with prediction, with the exception of the higher observed mortality around 18.75–18.99 invertebrates (only four nests).

Designed experiment

The initial analysis of the designed experiment showed a significant effect of proportion of foraging area sprayed ≤ 20 days before hatching ($F_{1,59} = 10.64, P < 0.001$), but effects of site and proportion of foraging area sprayed > 20 days before hatching were not significant. The non-significant terms were dropped from the model and predictions made using just the significant covariate. There was a statistically significant effect of the proportion of the 200-m-



Figure 1. Observed values and fitted line for Yellowhammer brood reduction in response to the abundance of 'important' invertebrates. Observed values are plotted against mid-points of groupings; numbers next to observed data points indicate sample size (number of nests).

Table 2. Outcome of GLMs investigating the effect of food supply on Yellowhammer brood reduction, for (i) all invertebrate food, (ii) important invertebrate food and (iii) large (\geq 5 mm) invertebrate food.

GLM	Ζ	Р	df	Intercept	Pesticide coefficient
Farm + all invertebrates	-10.14	< 0.001	1	40.64	-2.203
Farm + important invertebrates	-11.34	< 0.001	1	40.41	-2.259
Farm + large invertebrates	-7.79	< 0.001	1	14.615	-0.9613

Table 3. Parameter estimates for models of effect of proportion of Yellowhammer foraging range sprayed with insecticide within 20 days of hatching on probability of brood reduction. Model 1 (n = 64) includes nests in which at least one chick survived to fledging; Model 2 (n = 95) includes all nests for which brood reduction was observed, some of which later suffered total loss through predation or starvation. Probability of brood reduction, P, at x = proportion sprayed ≤ 20 days from hatching, is given by $P = [e^{(a+bx)}]/[1 + e^{(a+bx)}]$.

		Model 1				Model 2			
Term	Estimate	se	t ₆₃	Anti-log of estimate	Estimate	s.e.	t ₆₃	Anti-log of estimate	
Constant (<i>a</i>) Slope (<i>b</i>)	-1.07 2.60	0.353 0.928	-3.02 2.80	0.344 13.5	-1.02 2.08	0.361 0.845	-2.83 2.46	0.359 8.00	

Table 4. Predicted values $(\pm se)$ for probabilities of Yellowhammer brood reduction in relation to proportion of the 200-m-radius foraging area sprayed \leq 20 days before hatching. Model 1 includes nests in which at least one chick survived to fledging; Model 2 includes all nests for which brood reduction was observed.

Proportion	Probability of brood reduction				
sprayed ≤ 20 days from hatching	Model 1	Model 2			
0.00	0.26 ± 0.07	0.35 ± 0.06			
0.25	0.40 ± 0.07	0.49 ± 0.06			
0.50	0.56 ± 0.09	0.62 ± 0.08			
0.75	0.71 ± 0.11	0.74 ± 0.09			
1.00	$\textbf{0.82}\pm\textbf{0.11}$	$\textbf{0.83}\pm\textbf{0.09}$			

radius foraging area sprayed with insecticide ≤ 20 days before hatching on brood reduction ($F_{1,59} = 8.86$, P = 0.003; Table 3, Fig. 2a). The second model, with the larger dataset, gave a very similar result ($F_{1,93} =$ 8.83, P = 0.003; Table 3, Fig. 2b). Model fits were tested using the Hosmer–Le Cessie omnibus lack of fit test for a binary logistic model (Hosmer *et al.* 1997), and no lack of fit was detected (Z = -0.65, P > 0.05, Model 1; Z = -0.57, P > 0.05, Model 2). Table 4 gives the predicted probabilities of brood reduction at different levels of insecticide use, for the two models.

Skylark

Data from RSPB studies

No pesticide predictors significantly influenced nestling condition of Skylarks monitored by the RSPB. However, there was some evidence of a relationship between the timing of insecticide application and nestling condition, with mean brood weight being lowest in nests in fields exposed to breeding season applications (Wald 1.90, P = 0.149, df = 2). Growth rates were not significantly correlated with pesticide application.



Proportion of 200 m range sprayed \leq 20 days from hatching

Figure 2. Logistic model and observed data for effects of proportion of foraging range sprayed with insecticide on brood reduction in Yellowhammer (a) in treated years for fledged nests (n = 64), and (b) in treated years for all nests with valid observations (n = 95).



Figure 3. Relationship between the abundance of Skylark chick food within 100 m of the nest and the mean chick mass per brood (g) at Days 5-9 since hatching. Partial regression plot; note standardized axes.

Data from the Allerton Trust, Loddington

At Loddington, there was a significant relationship between chick condition and chick food index (mean (\pm se) chick mass = 9.636 \pm 3.936 log chick food + 1.076 ± 0.300 tarsus length -59.565 ± 25.343 ; $F_{2.7} =$ 7.153, P = 0.020; Fig. 3). There was no significant relationship between growth rate and chick food index.

Corn Bunting

The initial model contained only one variable, the food index. Predicted values of the probability of brood survival to fledging varied from *c*. 0.5 to > 0.9over 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 (Fig. 4). The fitted relationship was: $\ln(P(1 - P(1 - P(1$ P) = ln(x + 1) * 0.9623 + 0.1385 (deviance test P < 0.05, df = 1), where P = probability of success and x is the abundance of invertebrates as calculated using the method described in Brickle et al. (2000).

A follow-up model included a year factor and indicated that the relationship between brood survival and food abundance varied between the two years when the data were collected. However, the interaction term between year and food was not significant, i.e. the slopes of the relationships in the two years were similar, but the intercepts were different.



regression model relating probability of fledging to chick food index for Corn Bunting. Observed values are plotted against midpoints of groupings; numbers next to observed data points indicate sample size (number of nests). See Brickle et al. (2000) for method of calculation of chick food index.

12

2.5

3

DISCUSSION

0.9 0.8

0.7

11

In the studies described above, we have identified and defined relationships between invertebrate abundance and chick condition or survival for three passerines: Yellowhammer, Corn Bunting and Skylark. In addition, new evidence is provided that the probability of brood reduction in Yellowhammer was related to the proportion of the foraging area around the nest which was sprayed with insecticide. Yellowhammers are known to forage in non-crop areas such as field margins as well as within crops (Perkins et al. 2002), but although such alternative habitats were available at the study sites, either the food resources were not adequate to offset the effects of the insecticide applications or the insecticides also affected invertebrate populations in the field margins. The analyses did not include any allowance for the amount of non-crop habitat available, but in most cases this is likely to have been similar between nests.

Further evidence obtained from analysis of a subsample of Yellowhammer nests from the Yorkshire experimental site, for which nest-specific invertebrate samples were available, showed significant relationships between insecticide use and chick food arthropods, between chick food arthropods and chick condition, between chick food arthropods and chick growth rate, and between chick growth rate and chick survival (J. Hart unpubl. data). Although no significant effects of pesticides on Skylark chick condition or growth rate were detected, sample sizes were small, and so it is not possible to rule these out.

Species	Effect of pesticides		Effect of chick food availability			
	Food abundance	Foraging behaviour	Chick condition	Chick growth rate	Brood size/ chick survival	Effect of breeding performance on population change
Grey Partridge ¹	*	*	*		*	*
Red-legged Partridge ²					*	
Pheasant ³	*				*	
Barn Swallow ⁴	NS	NS ^a				
Skylark ⁵			*	NS ^a	NS ^a	
Yellowhammer ⁶	*	*	*	*	*	
Corn Bunting ⁷	*	*	*		*	

Table 5. Evidence of effects of pesticides on farmland birds.

*Statistically significant effect demonstrated in at least one study; NS, study showed no significant effect.

¹Potts (1980, 1986), Green (1984), Potts and Aebischer (1991, 1995), Rands (1985, 1986).

³Hill (1985), Sotherton and Robertson (1990).

⁴Evans (2001).

⁵This paper.

⁶Morris et al. (2002, in press), this paper, and J. Hart (unpubl. data).

⁷Brickle et al. (2000) and this paper.

^aLack of statistical significance may be due to small sample size.

At Loddington, a significant relationship was detected between Skylark chick condition and the abundance of chick food invertebrates, in spite of the very small sample size (11 nests). Further data on Skylarks are required before firm conclusions can be drawn about potential effects of pesticide use.

Table 5 summarizes current knowledge derived from quantitative studies of the indirect effects of pesticides on bird species via impacts on chick food abundance. In addition to the galliforms Grey Partridge, Red-legged Partridge and Pheasant, there is now evidence that pesticide use can affect breeding performance of the passerine species Yellowhammer and Corn Bunting. However, studies on Barn Swallow *Hirundo rustica* showed no effects of pesticides on food taxa or foraging behaviour of this species (Evans 2001).

Effects of pesticides may still occur even when their effects are not readily apparent. For example, even where no effects on brood reduction occur, chicks that fledge in poor condition are likely to have a lower probability of post-fledging survival. Furthermore, with low probabilities of survival to the next breeding season, parent birds may compromise their own survival probability by working harder to feed their chicks when density of invertebrate prey is low (Bradbury *et al.* 2003).

Unfortunately, there are no studies that provide evidence to assess the relationship between breeding performance and population change for these species. Demographic analyses have been used to indicate the key demographic rates causing population change. On the basis of such analyses, changes in adult survival rates have been proposed as the causal factor in the decline of the Yellowhammer, although the demographic mechanisms are by no means certain. There are some aspects of these analyses that may cause difficulties in interpretation, for example the lack of data on post-fledging survival rates and numbers of breeding attempts, and the exclusion of density dependence from such analyses (Siriwardena *et al.* 2000). Furthermore, the source of data on breeding productivity used in these analyses was the BTO's Nest Record Scheme, which provides estimates of nest failure rates but does not provide data on partial brood loss.

Bradbury *et al.* (2000) found that Yellowhammer nest survival rates in Oxfordshire were high, but that productivity per pair was probably too low to maintain a stable population. In the current study, data from the designed experiment indicated that productivity per pair was lower at all three sites in the treatment year than the mean of 3.27 recorded by Bradbury *et al.* (2000) (J. Hart unpubl. data). Whereas Yellowhammers typically have two or three nesting attempts (Bradbury *et al.* 2000), Corn Buntings are now largely single brooded, at least in Sussex (Brickle & Harper 2002). Brickle (1999) modelled the population dynamics of Corn Buntings in Sussex, and concluded that productivity was the most likely cause of decline in his study area. Evidence of

²Green (1984).

indirect effects of pesticides was found in the same study, indicating that pesticides could have played a role in the Corn Bunting decline, at least in this area.

In the absence of direct relationships between breeding performance and population change, simple population models based on the types of relationship reported here could be used to model the potential impact of pesticides on population change under different scenarios, using estimated distributions of values from the literature for life-cycle stages for which data have not been collected. The predictions of such models could inform the development of a framework for risk assessment (Boatman *et al.* 2003).

Of the three main mechanisms identified in the introduction to this paper, through which pesticides may affect food availability for birds, the evidence presented here is concerned solely with Type 1 effects, i.e. the effects of insecticides acting directly on invertebrates eaten by birds. Evidence for Type 2 effects has only been convincingly demonstrated for the Grey Partridge. The use of herbicides affects the abundance of invertebrate prey (e.g. Moreby & Southway 1999, Hawes *et al.* 2003), but data are largely limited to empirical observations of relationships between weed and invertebrate abundance, and information needed for the construction of mechanistic models is generally lacking.

Herbicides also affect weed seed production, thereby potentially reducing the availability of seed food for granivorous bird species (e.g. Heard *et al.* 2003), resulting in possible Type 3 effects. Relationships between bird feeding densities and seed densities have been demonstrated for several species (e.g. Robinson & Sutherland 1999), but the implications for survival and population change remain unclear. Yellowhammers responded to the provision of supplementary seed in the designed experiment described above, in terms of numbers of feeding birds, and there was some evidence of greater settling densities in the following spring where seed was supplied (T. Milsom unpubl. data).

There is some evidence that population dynamics of Linnet Carduelis cannnabina and Turtle Dove *Steptopelia turtur* have been influenced by Type 3 indirect effects. The decline in the Linnet population coincided with reductions in the abundance of key weed species that provided the bulk of seeds for chicks, and preceded a dietary switch by Linnets to the unripe seeds of oilseed rape and dandelions (Moorcroft *et al.* 1997). The key weed species are known to be vulnerable to herbicides. Evidence for a demographic response by Linnets to changes or reductions in the availability of seeds for chicks is circumstantial: Linnet populations breeding in areas where oilseed rape and dandelions are scarce settle at low densities, breed later, and suffer high levels of brood reduction and of complete brood starvation (Moorcroft 2002).

Turtle Doves also feed extensively on weed seed supplies during the breeding season (Browne & Aebischer 2003) and may ultimately rely upon them. Several of the weed species that feature extensively in the Turtle Dove diet (e.g. Chickweed *Stellaria media*) have undergone widespread declines on farmland in Britain in recent years (Firbank & Smart 2002), and are susceptible to the frequency of herbicide use (Ewald & Aebischer 1999). It is probable that the reduction in the number of breeding attempts made each year may be responsible for the decline in Turtle Dove numbers (Browne & Aebischer 2004). The shortening of the breeding season may be the result of food shortages later in the summer but further work will be required to confirm this.

Table 6 compares the current situation, regarding evidence for indirect effects of pesticides, with the list of definite and potential effects presented by Campbell et al. (1997). The current list of species considered to be at risk from the indirect effects of pesticides differs significantly from that compiled by Campbell et al. (1997). Indirect effects on one species in the 'possible' category in Campbell's list, Barn Swallow, have been provisionally ruled out, whereas they have been demonstrated for two species on the 'qualified possible' list, Corn Bunting and Yellowhammer. Turtle Dove, which was not considered by Campbell et al., is provisionally identified as being at risk. Finally, the position of nine species on Campbell's list, five in the 'possible' category and four in the 'qualified possible' category, is unclear because the requisite data are still lacking.

A number of potential measures are available to offset indirect effects of pesticides. The most obvious is minimizing the use of potentially damaging pesticides. This applies particularly to insecticides, which are generally applied in response to a pest outbreak. Wherever possible, thresholds should be applied and spraying only carried out when pest levels exceed thresholds. In some cases, a choice of products is available, and in such cases, the product that is less toxic to non-target species is to be preferred. There may also be scope for altering the timing or dose applied to reduce impacts on non-target organisms.

Where there is use of products known to be harmful to bird food resources, measures to reduce impact **Table 6.** Comparison of lists compiled by Campbell *et al.* (1997), and the present status of evidence for species regarded as being at risk from the indirect effects of pesticides.

Species ¹	Campbell et al. ²	Current evidence ³
Grey Partridge Perdix perdix	Y	Y
Tree Sparrow Passer montanus	Р	(P)
Bullfinch Pyrrhula pyrrhula	Р	n.d.
Song Thrush Turdus philomelos	Р	n.d.
Lapwing Vanellus vanellus	Р	(N)
Reed Bunting Emberiza schoeniclus	Р	n.d.
Skylark Alauda arvensis	Р	Р
Linnet Carduelis cannabina	Р	(P)
Barn Swallow Hirundo rustica	Р	(N)
Blackbird Turdus merula	Р	n.d.
Starling Sturnus vulgaris	Р	n.d.
Corn Bunting Miliaria calandra	(P)	Y
Spotted Flycatcher Muscicapa striata	(P)	n.d.
Sand Martin Riparia riparia	(P)	n.d.
Mistle Thrush Turdus viscivorus	(P)	n.d.
Yellow Wagtail Motacilla flava flavissima	(P)	(P)
Dunnock Prunella modularis	(P)	n.d.
Yellowhammer Emberiza citronella	(P)	Y
Red-backed Shrike Lanius collurio	(P)	(P)
Turtle Dove Streptopelia turtur	-	(P)

¹Species order as given in Table 7.1 of Campbell *et al.* (1997). ²Quality of evidence for indirect effects (as given by Campbell *et al.* 1997): Y = definite effect; P = possible effect; (P) qualified possible effect; – not on list.

³Quality of evidence for indirect effects: Y = definite effect; P = possible effect; (P) circumstantial evidence for effect; (N) no evidence of effect from recent autecological studies; N = no effect, n.d. = no relevant data.

may be taken, such as leaving an untreated buffer zone around the edge of the field (mitigation), or alternative food-rich habitat may be provided (compensation). An example of the former is the use of unsprayed or 'conservation' headlands around cereal fields, which have been shown to increase the survival of Grey Partridge chicks (Rands 1985, 1986). A number of suitable measures are now funded by the European Union and national governments under agri-environment schemes.

CONCLUSIONS

Campbell *et al.* (1997) concluded that there was strong evidence that pesticides affected population change for only one species, the Grey Partridge. There is now good evidence that insecticides applied during the breeding season can affect breeding performance of at least two further species (Corn Bunting and Yellowhammer). Indications of possible effects on a third (Skylark) need to be confirmed through the collection of further data.

The data presented here, combined with evidence from the literature, demonstrate that indirect effects of pesticides do occur, although, apart from the Grey Partridge, unequivocal evidence is only available for effects of insecticides. There is, however, strong circumstantial evidence for effects of herbicides, from a variety of sources; unfortunately practical difficulties in demonstrating indirect effects arising from herbicides have prevented their confirmation so far. It remains unclear how important indirect effects of pesticides are in relation to other factors affecting populations of farmland birds. Further work is required to investigate the likely impact of the results presented here at the population level. However, it seems probable that indirect effects of pesticides form part of a suite of causal factors likely to be implicated in the declines of farmland bird species.

We wish to thank all the farmers, landowners and spray contractors who allowed access to their land and provided spraying records. We also thank Dr Nicholas Aebischer and two anonymous referees for helpful comments on the manuscript. The work was funded by Defra Pesticides Safety Directorate, apart from the research on Corn Bunting, which was funded by English Nature and the RSPB.

REFERENCES

- Boatman, N.D., Hart, A., Clook, M., Brown, V.K., Holland, J.M.
 & Lutman, P.J. 2003. A risk assessment framework for determining the effects of pesticides on farmland biodiversity. BCPC Int. Congr. Crop Sci. Technol. 2003: 239–244.
- Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J.
 & Wilson, J.D. 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. J. Appl. Ecol. 37: 789–805.
- Bradbury, R.B., Wilson, J.D., Moorcroft, D., Morris, A.J. & Perkins, A.J. 2003. Habitat and weather are weak correlates of nestling condition and growth rates of four UK farmland passerines. *Ibis* 145: 295–306.
- Brickle, N.W. 1999. The effect of agricultural intensification on the decline of the Corn Bunting, Miliaria calandra. DPhil thesis. University of Sussex.
- Brickle, N.W. & Harper, D.G.C. 2002. Agricultural intensification and the timing of breeding of Corn Buntings *Miliaria calandra*. *Bird Study* **49**: 219–228.
- Brickle, N.W., Harper, D.G.C., Aebischer, N.J. & Cockayne, S.H. 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. J. Appl. Ecol. 37: 742–755.
- Browne, S.J. & Aebischer, N.J. 2003. Habitat use, foraging ecology and diet of Turtle Doves *Streptopelia turtur* in Britain. *Ibis* 145: 572–582.

- Browne, S.J. & Aebischer, N.J. 2004. Temporal changes in the breeding ecology of European Turtle Doves *Streptopelia turtur* in Britain, and implications for conservation. *Ibis* 146: 125–137.
- Burn, A.J. 2000. Pesticides and their effects on lowland farmland birds. In Aebischer, N.J., Evans, A.D., Grice, P.V. & Vickery, J.A. (eds) *Ecology and Conservation of Lowland Farmland Birds*: 89–104. Tring: British Ornithologists' Union.
- Campbell, L.H., Avery, M.I., Donald, P., Evans, A.D., Green, R.E.
 & Wilson, J.D. 1997. A Review of the Indirect Effects of Pesticides on Birds. JNCC Report 227. Peterborough: Joint Nature Conservation Committee.
- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C.
 & Shrubb, M.J. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl. Ecol. 37: 71–788.
- Donald, P.F., Green, R.E. & Heath, M.F. 2001a. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. Royal Soc. Lond. B* 268: 25–29.
- Donald, P.F., Muirhead, L.B., Buckingham, D.L., Evans, A.D., Kirby, W.B. & Gruar, D.J. 2001b. Body condition, growth rates and diet of Skylark *Alauda arvensis* nestlings on lowland farmland. *Ibis* 143: 658–669.
- Donald, P.F., Evans, A.D., Muirhead, L.B., Buckingham, D.L., Kirby, W.B. & Schmitt, S.I.A. 2002. Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis* 144: 652–664.
- **Evans, K.L.** 2001. *The effects of agriculture on Swallows*, Hirundo rustica. PhD thesis, University of Oxford.
- Ewald, J.A. & Aebischer, N.J. 1999. *Pesticide Use, Avian Food Rresources and Bird Densities in Sussex*. Peterborough: Joint Nature Conservation Committee.
- Ewald, J.A., Aebischer, N.J., Brickle, N.W., Moreby, S.J., Potts, G.R. & Wakeham-Dawson, A. 2002. Spatial variation in densities of farmland birds in relation to pesticide use and avian food resources. In Chamberlain, D. & Wilson, A. (eds) Avian Landscape Ecology-Pure and Applied Issues in the Large-Scale Ecology of Birds: 305–312. IALE.
- Firbank, L.G. & Smart, S. 2002. The changing status of arable plants that are important food items for farmland birds. *Aspects of Applied Biology 67, Birds and Agriculture* 67: 165–170.
- Francis, B., Green, M. & Payne, C. 1993. *The GLIM System*. Release 4 Manual. Oxford: Clarendon Press.
- Fuller, R.J. 2000. Relationships between recent changes in lowland British agriculture and farmland bird populations: an overview. In Aebischer, N.J., Evans, A.D., Grice, P.V. & Vickery, J.A. (eds) *Ecology and Conservation of Lowland Farmland Birds*: 5–16. Tring: British Ornithologists' Union.
- Green, R.E. 1984. The feeding ecology and survival of partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in East Anglia. *J. Appl. Ecol.* **21**: 817–830.
- Gregory, R.D., Noble, D.G. & Custance, J. 2004. The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. In *Ecology and Conservation of Lowland Farmland Birds II: The Road to Recovery. Ibis* **146** (Suppl. 2): 1–13.
- Hawes, C., Haughton, A.J., Osborne, J.L., Roy, D.B., Clark, S.J., Perry, J.N., Rothery, P., Bohan, D.A., Brooks, D.R., Champion, G.T., Dewar, A.M., Heard, M.S., Woiwod, I.P., Daniels, R.E., Young, M.W., Parish, A.M., Scott, R.J., Firbank, L.G. & Squire, G.R. 2003. Responses of plants and

invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Phil. Trans. Royal Soc. Lond. B* **358**: 1899–1913.

- Heard, M.S., Hawes, C., Champion, G.T., Clark, S.J., Firbank, L.G., Haughton, A.J., Parish, A.M., Perry, J.N., Rothery, P., Scott, R.J., Skellern, M.P., Squire, G.R. & Hill, M.O. 2003. Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. I. Effects on abundance and diversity. *Phil. Trans. Royal Soc. Lond. B* **358**: 1819–1832.
- Hill, D.A. 1985. The feeding ecology and survival of pheasant chicks on arable farmland. J. Appl. Ecol. 22: 645–654.
- Hosmer, D.W., Hosmer, T., le Cessie, S. & Lemeshow, S. 1997. A comparison of goodness-of-fit tests for the logistic regression model. *Statistics Med.* 16: 965–980.
- Moorcroft, D. 2002. Linnet. In Assessing the Indirect Effects of Pesticides on Birds. Unpublished report to Defra. Sandy: RSPB.
- Moorcroft, D., Bradbury, R.B. & Wilson, J.D. 1997. The diet of nestling Linnets Carduelis cannabina before and after agricultural intensification. Brighton Crop Protection Conference – Weeds: 923–928. Farnham: British Crop Protection Council.
- Moreby, S.J. & Southway, S.E. 1999. Influence of autumn applied herbicides on summer and autumn food available to birds in winter wheat fields in southern England. *Agric. Ecosyst. Environ.* **72**: 285–297.
- Morris, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Kyrkos, A., Buckingham, D.L. & Evans, A.D. 2001. Foraging habitat selection by Yellowhammers (*Emberiza citrinella*) in agriculturally contrasting regions in lowland England. *Biol. Conserv.* 98: 197–210.
- Morris, A.J., Bradbury, R.B. & Wilson, J.D. 2002. Indirect effects of pesticides on breeding yellowhammers *Emberiza citrinella*. *BCPC Conf.* – *Pests Dis.* **2002**: 965–970.
- Morris, A.J., Wilson, J.D., Whittingham, M.J. & Bradbury, R.B. 2004. Evidence for indirect effects of pesticides on breeding yellowhammers *Emberiza citrinella*. Agric. Ecosyst. Environ. in press.
- Murray, K.A. 2004. Factors affecting foraging by breeding farmland birds. PhD thesis, Harper Adams University College.
- Newton, I. 1995. The contribution of some recent research on birds to ecological understanding. J. Anim. Ecol. 64: 675–696.
- **Newton, I.** 2004. The recent declines of farmland bird populations in Britain. An appraisal of causal factors and conservation actions. *Ibis* **146**: 579–600.
- O'Connor, R.J. 1984. Behavioural regulation of bird populations: a review of habitat use in relation to migration and residency. In Sibly, R.M. & Smith, R.H. (eds) *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour:* 25th Symposium of the British Ecological Society: 105–142. Oxford: Blackwell Scientific Publications.
- Perkins, A.J., Whittingham, M.J., Morris, A.J. & Bradbury, R.B. 2002. Use of field margins by foraging yellowhammers. *Agric. Ecosyst. Environ.* **93**: 413–420.
- Potts, G.R. 1980. The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Adv. Ecol. Res.* 11: 1–79.
- Potts, G.R. 1986. The Partridge: Pesticides, Predation and Conservation. London: Collins.
- Potts, G.R. & Aebischer, N.J. 1991. Modelling the population dynamics of the Grey Partridge: conservation and management.

In Perrins, C.M., Lebreton, J.-D. & Hirons, G.J.M. (eds) *Bird Population Studies: Their Relevance to Conservation and Management*: 373–390. Oxford: Oxford University Press.

- Potts, G.R. & Aebischer, N.J. 1995. Population dynamics of the Grey Partridge *Perdix perdix* 1793–1993: monitoring, modelling and management. *Ibis* 137: S29–S37.
- Poulsen, J.G., Sotherton, N.W. & Aebischer, N.J. 1998. Comparative nesting and feeding ecology of skylarks *Alauda arvensis* on arable farmland in southern England with special reference to set-aside. *J. Appl. Ecol.* **35**: 131–147.
- Rands, M.R.W. 1985. Pesticide use on cereals and the survival of Grey Partridge chicks: a field experiment. *J. Appl. Ecol.* **22**: 49–54.
- Rands, M.R.W. 1986. The survival of gamebird (Galliformes) chicks in relation to pesticide use on cereals. *Ibis* **128**: 57–64.
- Robinson, R.A. & Sutherland, W.J. 1999. The winter distribution of seed-eating birds: habitat structure, seed density and seasonal depletion. *Ecography* 22: 447–454.
- Robinson, R.A., Hart, J.D., Holland, J.M. & Parrott, D. 2004. Habitat use by seed-eating birds: a scale-dependent approach. *Ibis* **146**: 88–99.
- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. 1998a. Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Bird Census indices. J. Appl. Ecol. 35: 24–43.

Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. 1998b. Variation

in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study* **45**: 276–292.

- Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P., Wilson, J.D. & Gates, S. 2000. The demography of lowland farmland birds. In Aebischer, N.J., Evans, A.D., Grice, P.V. & Vickery, J.A. (eds) *Ecology and Conservation of Lowland Farmland Birds*: 117–133. Tring: British Ornithologists' Union.
- Sotherton, N.W. & Robertson, P.A. 1990. Indirect impacts of pesticides on the production of wild gamebirds in Britain. In Church, K.E., Warner, R.E. & Brady, S.J. (eds) *Perdix V, Gray Partridge and Ring-necked Pheasant Workshop*: 84–102. Emporia: Kansas Department of Wildlife and Parks.
- Stephens, P.A., Freckleton, R.P., Watkinson, A.R. & Sutherland, W.J. 2003. Predicting the response of farmland bird populations to changing food supplies. J. Appl. Ecol. 40: 970–983.
- Stoate, C., Moreby, S.J. & Szczur, J. 1998. Breeding ecology of farmland Yellowhammers *Emberiza citrinella*. *Bird Study* 45: 109–121.
- Welham, S. 1993. Procedure GLMM. Genstat 5 Procedure Library Manual. Oxford: NAG.
- Wilson, J.D., Arroyo, B.E. & Clark, S.C. 1996. The Diet of Bird Species of Lowland Farmland: a Literature Review. Unpublished report to the Department of the Environment and Joint Nature Conservation Committee. Sandy: University of Oxford & Royal Society for the Protection of Birds.