Linking agricultural practice to insect and bird populations: a historical study over three decades

TIM G. BENTON*, DAVID M. BRYANT*, LORNA COLE*‡ and HUMPHREY Q. P. CRICK†

IBIS, University of Stirling, Stirling FK9 4LA, UK; and †British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

Summary

1. There is continuing debate about the impact of agricultural practices on farmland wildlife. In particular, it has been postulated that a general decline in insect abundance linked with intensification of agriculture may have contributed to farmland bird decline. While some autecological studies have supported this hypothesis, larger-scale and long-term studies are needed.

2. Suction traps mounted on 12·2-m towers (Rothamsted-type) have been sampling aerial insects for nearly 40 years throughout the UK. Their catches are correlated over large spatial scales. We analysed insect catch data from a single suction trap run for 27 years in a rural location in Scotland, and showed that insect numbers have changed significantly over time, although non-linearly. The multivariate data set (numbers from the 12 common arthropod groups) was summarized using principal components analysis (PCA) to extract three components explaining 62% of the variation.

3. We also used PCA to describe agricultural change, using published agricultural data for eight measures of farming in Scotland. Arthropod abundance and principal component (PC) scores were significantly related to the agricultural PC scores as well to summary climatic measures.

4. Using Scottish data from the British Trust for Ornithology Common Birds Census, we extracted three PC to describe the time-dependent average densities of 15 common farmland birds in Scotland. Measures of bird density were significantly related to insect abundance and PC scores and, independently, to measures of agriculture and climate.

5. These data from a broad suite of species provide support for linked temporal change between farmland birds, invertebrate numbers and agricultural practice in Scotland. Although entirely correlative, the results are consistent with the view that agricultural change has influenced birds through changes in food quality or quantity. The work also shows how large-scale invertebrate sampling, in this case using suction traps, is useful for monitoring farmland biodiversity.

Key-words: farming, farmland, generalized additive models, population trend, suction trap.

Journal of Applied Ecology (2002) **39**, 673–687

Introduction

Agricultural practice has changed markedly in the past 50 years in Britain, as elsewhere (Blaxter & Robertson 1995). For example, wheat yields in Scotland during the period between 1967 and 1999 have increased by 201% due to a combination of more efficient tillage, application of fertilizers and pesticides, and plant breeding (Gardner 1996). Large changes to the farmed landscape have occurred at two scales. First, fields have been amalgamated to allow efficient farming and so the area of non-crop land has been reduced (Gardner 1996; Harvey 1997; Krebs *et al.* 1999). Secondly, changes in agricultural practice have allowed crops to be kept largely weed- and pest-free, mainly through the use of pesticides. In 1996, in addition to fertilizers, an average Scottish cereal field was spayed 6·5 times, with some spays including a mixture of different pesticides, at a

Correspondence: Tim G. Benton, IBIS, University of Stirling, Stirling FK9 4LA, UK (fax 01786 464994; e-mail tgb1@stir.ac.uk).
‡Current address: Scottish Agricultural College, Auchincruive, Ayr KA6 5HW, UK.

rate of 2·6 kg of active ingredient per hectare (Snowden & McCreath 1997).

Such changes affect the habitats of non-agricultural species, such as birds. Between 1970 and 1990, 86% (*n* = 28 species) of UK farmland birds had reduced distributions and 83% (*n* = 18) had declined in abundance (Fuller *et al*. 1995). Siriwardena *et al*. (1998) confirmed a decline in abundance of 11 of 13 specialist farmland birds, on average to 52% of the population size of 1968. Broadly similar patterns of decline have been shown for insects (Aebischer 1991; Woiwod 1991), arachnids (Aebischer 1991) and arable weeds (Sotherton 1998).

The decline in farmland bird populations has accompanied farming intensification (Fuller *et al*. 1995; Chamberlain *et al*. 2000). However, the mechanism by which farming practice influences bird populations is debated (Campbell *et al*. 1997; Gillings & Fuller 1998; Siriwardena *et al*. 1998, 2000; Moreby & Southway 1999; Freemark & Kirk 2001; Vickery *et al*. 2001). Recent studies suggest that reduced food supplies may reduce survival (Wilson *et al*. 1997; Payne & Wilson 1999; Peach, Siriwardena & Gregory 1999; Wilson *et al*. 1999; Siriwardena *et al*. 2000; Vickery *et al*. 2001). A link between arthropod availability and population size is known for grey partridge (Southwood & Cross 1969), and may be important in other bird species (Bryant 1973; Turner 1980; McCracken & Foster 1994; Wilson *et al*. 1997; Laiolo & Rolando 1999; Brickle *et al*. 2000). Wilson *et al*. (1999) showed that declining 'granivorous' birds relied significantly more on insect food than those not in decline. Therefore, an important factor influencing bird declines may be that changes in farming practice alter the availability of insect food (Vickery *et al*. 2001).

The value of arthropods as a food for birds will be determined by the costs of searching as well as the nutritional benefit gained from their ingestion. When arthropods are rare, parental birds may work harder to get the same or a reduced amount of food for their chicks (Brickle *et al*. 2000; Morris *et al*. 2001). The increased costs of foraging can have immediate consequences (through chick starvation or smaller clutches) or the effect may be delayed (slower growth, reduced over-winter survival of both juveniles and adults, reduced fecundity the following year) (Holmes 1995; Siriwardena *et al*. 2000).

Given these issues, a variety of predictions are possible. First, if farming has been important in affecting food supplies for birds, measures of arthropod abundance should be related to measures of farming practice, both at the current time and with a lag; most insects have an annual life cycle, so insect numbers in year *t* may depend on environmental conditions at *t* − 1. Secondly, measures of bird abundance should also be related to measures of farming practice (both current and in the previous year, as population size at *t* is influenced by productivity in *t* − 1). Thirdly, bird abundance should be related to arthropod abundance

both in the current and previous year due to delays in life-history effects.

To investigate these predictions requires information on birds, arthropod populations and farming over time. Long-term data on the abundance of insects has rarely been collated or reported (although see Aebischer 1991; Woiwod 1991). Since 1972, a single 12·2-m suction trap has sampled insects with constant effort throughout the summer months on the rural campus of the University of Stirling, Stirling, UK. Comparison of the measures of insect abundance with published information from agricultural censuses and data on bird populations [British Trust for Ornithology (BTO) Common Bird Census] allows potential associations to be identified.

Materials and methods

INSECT SUCTION TRAP DATA

A Rothamsted-type 12·2-m high suction trap (Macaulay, Tatchell & Taylor 1988) has operated at the farmland edge of the University of Stirling campus since 1972 (grid reference NS812967, 56°08′54″ latitude, −3°54′45″ longitude). Captured arthropods fall into alcohol and are removed daily at 9:00 from April to October. We sorted a median of 44 (range 34–45) sample days per year, from 1972 to 1998, from the same calendar days spread equally throughout the period April to September The difference in sample sizes from year to year was a consequence of lost data or samples that were in too poor a state to sort. A total of 1139 samples was sorted into 15 orders (Acari, Aranaea, Coleoptera, Collembola, Diptera, Ephemeroptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, Neuroptera, Plecoptera, Psocoptera, Thysanoptera, Trichoptera). The median catch size for Neuroptera, Plecoptera and Trichoptera was zero, so these orders were excluded from analysis.

IDENTIFICATION OF TRENDS IN THE ARTHROPOD GROUPS

Following Fewster *et al*. (2000), we identified trends using generalized additive models (GAMs) (Hastie & Tibshirani 1990), coupled with bootstrap inference. GAMs are a form of non-parametric regression, useful for identifying trends in time-series data where such trends may not be well predicted by parametric regressions. We used smoothing splines to fit the data. These are locally cubic splines that minimize a penalized residual sum of squares, and describe a smoothed curve through the data points. The degree of smoothness is specified in terms of degrees of freedom: with low degrees of freedom the line tends to linearity; with high degrees of freedom the line tends towards connecting each datum. Analysis of deviance can be used to test whether the 'curviness' of the GAM significantly improves the fit over a linear regression (i.e. a straight

line). Following Fewster *et al.* (2000), we use the term 'trend' to refer to the year effect from a GAM, rather than as a linear measure of change over time, because linear trends may miss important detail over a smaller subset of years. Identification of trends in time-series is somewhat subjective, in that the underlying pattern is being separated from year-to-year noise. Automated model-selection routines, such as minimizing the Aikake information criterion (AIC) statistic, may over-fit the data, in that they specify models which tend to be more 'jagged' than necessary for trend identification. Fewster *et al.* (2000) recommend visually varying the degrees of freedom until the trend line obviously starts picking up the noisiness of the annual variations, up to $n/3$–$n/2$ degrees of freedom. We used GAMs that fitted a day-within-year effect simultaneously with a year effect (see below for a detailed example). Firstly, as with generalized linear modelling (GLM), we chose a modelling family by specifying the error structure and link function. We then initially chose a model based on minimizing the AIC statistic, by specifying models with different degrees of freedom (up to 12 for the year and day effects). The fits of this model were inspected visually to ensure that the model was not too overfitted according to Fewster *et al.*'s (2000) criterion. Residuals and fits were inspected throughout to ensure the model did not invalidate assumptions about the distributions of residuals. The trends reported here are the partial fits for the year effect, scaled such that at year zero (1972) the abundance = 1. We used bootstrap resampling to estimate confidence intervals for the trends (James, McCulloch & Wiedenfield 1996; Fewster *et al.* 2000). Five-hundred bootstrap resamples of the data were taken (by randomly selecting from each month's samples along the time-series). To each sample the GAM model was fitted and the trend line identified. The quantiles of the partial fits for the year effect from the 500 GAMs were used to estimate the confidence intervals (CI). All the GAM modelling and resampling was conducted using the Splus 2000 statistical package (Mathsoft Inc., Seattle, WA).

CLIMATIC VARIABLES

Changes in the number of insects or birds over time could be caused by climatic changes. Rather than include a multitude of climate variables in our analyses we used two factors that strongly reflect the daily climate: the annual values of the North Atlantic oscillation (NAO) and the northern hemisphere temperature anomalies (NHA). The NAO is a large-scale pattern of natural climate variability that has important impacts on the weather and climate of the North Atlantic region and surrounding continents, especially Europe (Osborn 2000). The NHA is the time-series of the northern hemisphere's annual anomalies from the long-term average near-surface temperature (Jones *et al.* 1999). Both the NAO and NHA capture much of the variability in climate measured locally. To show

this, we used 'best subsets' regression to relate the annual values of the NAO and NHA to subsets of 36 climatic variables from a meteorological recording station on the University of Stirling campus over the 27 years of the study. For the NAO this procedure selected a model relating March, May, June and September temperatures and June and July rainfall (adjusted $R^2 = 84.5\%$). For the NHA the selected model included 11 variables (February, March, October temperature; March, August and November hours of sun; January, March, April, June and October rain) and had an adjusted R^2 of 93·7%. The NHA trend has been upwards in recent decades, so is a record of global warming (Jones *et al.* 1999).

BIRD COUNTS

Count data from the BTO's Common Birds Census (Marchant *et al.* 1990) were used to estimate bird population densities in the analyses. Data are sparse from farmland plots in lowland Scotland during the period of the study, especially prior to 1979. From 1979 to 1997 there was an average of five plots per year [range 3–7, median 5, interquartile (IQ) range 4–6], therefore providing the most reliable information. Birds that were uncommon (with a median count of 0 across sites and years) were excluded, leaving the following 15 species of farmland birds: chaffinch *Fringilla coelebs* L., carrion crow *Corvus corone* L., dunnock *Prunella modularis* (L.), greenfinch *Carduelis chloris* (L.), lapwing *Vanellus vanellus* (L.), oystercatcher *Haematopus ostralegus* L., grey partridge *Perdix perdix* (L.), linnet *Carduelis cannabina* (L.), meadow pipit *Anthus pratensis* (L.), robin *Erithacus rubecula* (L.), skylark *Alauda arvensis* L., starling *Sturnus vulgaris* L., swallow *Hirundo rustica* L., wren *Troglodytes troglodytes* (L.), and yellowhammer *Emberiza citrinella* L. Territory clusters per plot were converted to territories per hectare before analysis.

AGRICULTURE

Agricultural data were obtained for 1972–97, principally from the annual *Economic Reports on Scottish Agriculture* (called *Agricultural Statistics for Scotland* before 1980 and published by the Department of Agriculture and Fisheries for Scotland) and reports on *Pesticide Usage in Scotland* (Snowden & McCreath 1997). The following 28 time-series were obtained: area of rough grazing; combined area of crops and grassland; number of cattle, sheep and pigs; number of full-time, part-time and casual workers; tonnes of wheat, barley, oats and oilseed rape produced and area of each crop grown; inputs of nitrogen, potassium and phosphate fertilizer, lime, insecticide, seed-dressing, fungicide, herbicide, growth regulator and total pesticides used (all in tonnes of active ingredients); the amount of agricultural land lost and the percentage of cereal spring sown.

IDENTIFYING PATTERNS OF ASSOCIATION BETWEEN AGRICULTURE, ARTHROPODS AND BIRDS

Given the multivariate measures of agricultural practice, arthropod and bird numbers, we used principal components analysis (PCA) to reduce the number of variables. PCA can be conducted as long as there are fewer variables than data, but higher ratios of data to variables are widely recommended. We therefore removed agricultural variables that were collinear (e.g. the yields of wheat, barley and oats, and the amount of fertilizer applied, are all positively correlated) or were inconsistent through time (one kilogram of insecticide had very different properties in 1997 and 1972) or had missing data. We retained the following eight variables: the amount of crops and grazing land in Scotland; the numbers of cattle and of part-time workers; the yield of wheat; the loss of agricultural land each year; the total amount of cereal grown and the amount which was spring sown; and the production of rape per year. PCA was conducted on the correlation matrix between these variables and the yearly 'scores' for the first three components extracted (cf. Chamberlain *et al.* 2000).

We summarized the data for the arthropods and birds in two ways. First, the numbers over time were summarized (as the mean or standard deviation of the data or the trends). Secondly, PCA was conducted on the extracted trends for the 12 arthropod groups, or on the raw data for the 15 bird species. We conducted two PCA analyses: one using all 26 years of data (and discarding the pre-1979 scores) and one on the post-1979 data alone.

With fewer summary variables (three PCA scores, or summary statistics of the distribution of animals) the associations between agriculture, arthropods and birds

could be explored using MANOVA and 'best subsets regression'. The PCA analysis and subsequent analysis was conducted using MINITAB (Minitab Inc., PA, USA).

Results

TRENDS IN ARTHROPODS

Example analysis: fly numbers since 1972

Insect numbers change both within and between years. The data were modelled using GAMs of the form:

$$\text{numbers} = \text{spline(day-within-year, d.f. } d) + \text{spline(year, d.f. } y) + \text{error}$$

The number of insects in a sample cannot be negative, hence a log-link function is required. The distribution of counts across days was usually overdispersed: some days had very large numbers, others had very few, such that the variance was often proportional to the square of the mean value. The degree of overdispersion required quasi-likelihood estimations of the regression parameters, with a log-link function (McCullagh & Nelder 1989). This fits the parameters of the model, when the error distribution is not fully known, using iteratively reweighted least squares, once the link-function and variance functions have been supplied (S-plus 2000). The fly counts over 27 years were fitted in this way. Varying the degrees of freedom for the spline varied the degree of smoothing and hence the fit (Table 1). Day-within-year effects were significantly non-linear, and most efficiently fit by a 6 d.f. spline (i.e. a 6 d.f. spline minimized AIC). The optimum fit for the trend (the year effect) was not so clear (Fig. 1). The model with the minimum AIC had the maximum degrees of freedom for the year effect spline because it was fitting

Table 1. Statistics for different GAMs fitted to the 1139 fly counts from a suction trap at Stirling University, UK, from 1972 to 1998. Models of the form flies = s(year, d.f. = y) + s(day-within-year, d.f. = d) were fitted using a log-link function, variance proportional to μ^2 and quasi-likelihood estimation (using the Splus GAM routines). P s(year) and P s(dayinyr) refer to the significance of the smoothing splines fitted to the year and day-within-year effects in the model; when $P < 0.05$ the spline indicates significant non-linearity. $P = 0$ indicates that the estimated probability approximates zero. Based on our criteria, the best model is the one fitting 12 d.f. splines to the year effect and 6 d.f. splines to the day-within-year effect

Terms of GAM for flies	Residual d.f.	Residual deviance	AIC	P s(year)	P s(dayinyr)
(null)	1138	1091			
s(year,12)	1126	1020·3	1037·9	1e−6	
s(year,12) + dayinyr	1125	843·1	862·1	6e−7	
s(year,12) + s(dayinyr,3)	1123	780·1	801·8	3e−7	0
s(year,12) + s(dayinyr,6)	1120	762·2	788·0	7e−8	0
s(year,12) + s(dayinyr,9)	1117	760·0	789·7	4e−8	0
s(year,12) + s(dayinyr,12)	1114	758·8	792·6	4e−8	0
s(dayinyr,6)	1132	817·3	826·8		
year + s(dayinyr,6)	1131	800·9	811·8		
s(year,3) + s(dayinyr,6)	1129	795·9	809·5	0·032	0
s(year,6) + s(dayinyr,6)	1126	781·5	799·2	0·00007	0
s(year,9) + s(dayinyr,6)	1123	771·2	792·9	2e−6	0
s(year,12) + s(dayinyr,6)	1120	762·2	788·0	7e−8	0
s(year,26) + s(dayinyr,6)	1106	735·1	775·6	1e−11	0
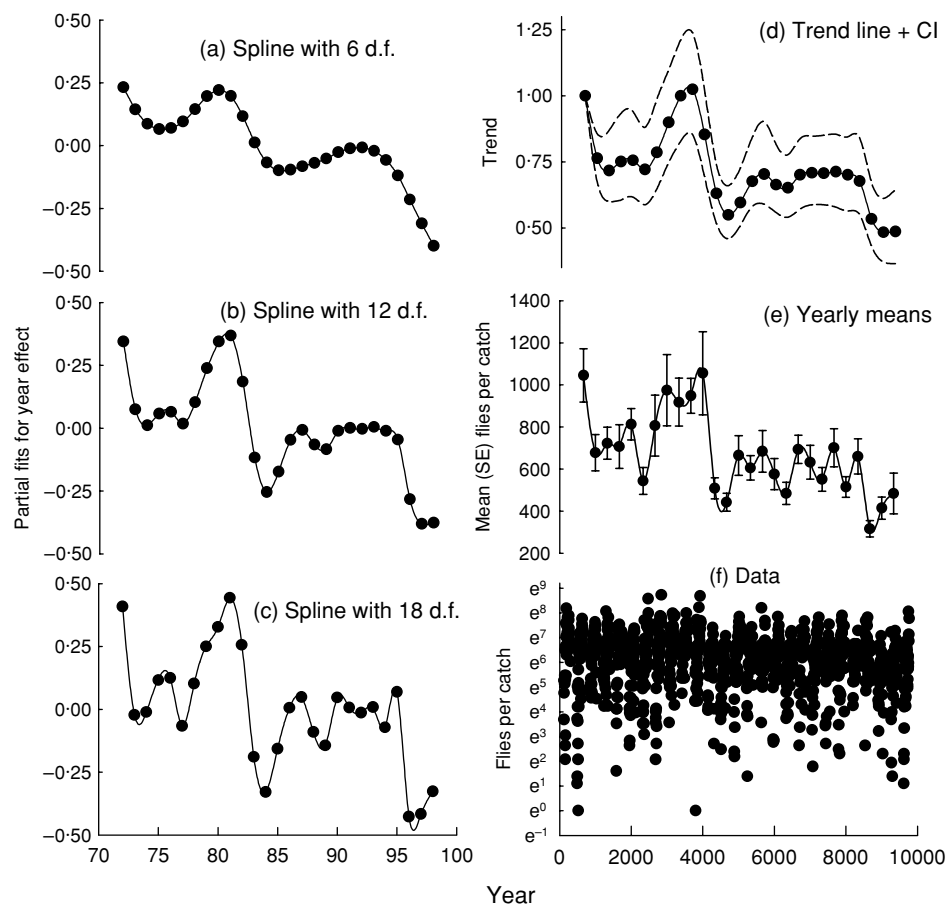
Fig. 1. An example of extracting a 'trend': long-term changes in the number of flies caught over 27 years by a suction trap at Stirling University, UK. The trend is the partial fits for year within a GAM. A spline with (a) 6 d.f.; (b) 12 d.f.; (c) 18 d.f. As the d.f. for the spline increases, the smoothed curve follows the data ever more closely, and the year to year variation begins to mask the underlying 'trend'. For this example a 12 d.f. spline was chosen as the best model of the trend, shown in (d). The partial fits are standardized so year 1 = 1 and confidence intervals are estimated by bootstrapping. (e) The mean counts (error bars are SE) for the 44 trap counts in each year. (f) The raw counts (numbers per day).

the mean of each year maximally. However, a trend describes the underlying pattern across years rather than purely the year-to-year variation. Fewster *et al.* (2000) recommend examining the partial fits for the year effect and choosing the appropriate degree of freedom on where the trend starts reflecting the yearly noise. This normally occurs with degrees of freedom between a third and a half of maximum (Fewster *et al.* 2000). We selected 12 d.f. as the best degree of smoothing.
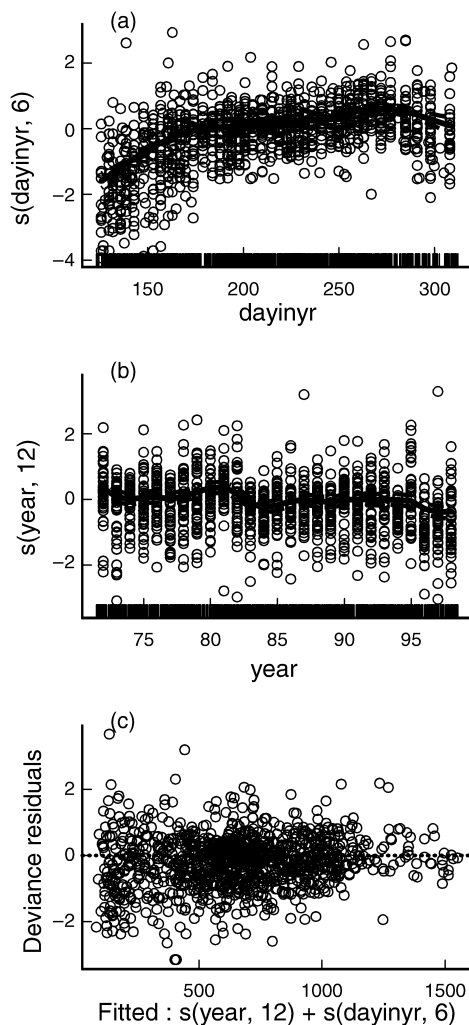
fly counts = s(year,12) + s(day-within-year,6).

The partial fits for year and day effects are the 'trends' within the year and between years, respectively (Fig. 2). This GAM was then fitted to bootstrap resamples to generate confidence limits for the trend. Trends were standardized by scaling them to start at 1·0, to allow comparison between arthropod groups.

Patterns of change in arthropods

The abundance of most arthropod taxa changed during the period 1972–98 (12/15 orders, total numbers

and volume; 7/8 beetle families and 13/18 fly families) (Fig. 3). Approximately 20% of groups did not change significantly over time even though the changes were considerable, mainly due to sparse data causing wide confidence intervals. Many trends were non-linear, with periods of high abundance (e.g. early mid-1980s) and periods of low abundance (the late 1970s and 1990s). For the 15 orders, the average abundance in 1997 (as a fraction of 1972) was 0·515 ± 0·115 (using total numbers caught) or 0·517 ± 0·108 (using index trends).

PCA on the 12 common arthropod groups gave three components with eigenvalues > 1, and these accounted for 29%, 19% and 14% of the variance, respectively (Fig. 4). PC1 described groups that fluctuated over time but ended with similar catch densities (e.g. beetles, spiders and Hymenoptera; Fig. 3 and Table 2). A higher PC1 score correlated with more arthropods. PC1 was also correlated with summer temperatures. PC2 described groups that declined, or rose, strongly (flies, Collembola, total numbers and volumes of insects); PC2 also correlated with the rise in NHA. A positive correlation with PC2 indicated a decline over

Fig. 2. The residuals and partial fits for the fly model discussed in Fig. 1. (a) The residuals around the fitted day-within-year effect (a 6 d.f. spline); (b) the residuals around the fitted year effect (a 12 d.f. spline); (c) the residuals vs. the fits. The trend is the partial fits for the year effect, shown as the line in (b).

The agricultural variables changed markedly over the study (Fig. 5). PCA extracted three variables, which accounted for 59·7%, 17·3% and 11·6% of the variation in the data (Fig. 4). PC1 correlated strongly with the first axis ($r = 0·95$, $n = 22$, $P < 0·0001$) identified by Chamberlain *et al.* (2000) from an analysis of data from England and Wales, and interpreted as measuring farming intensity. PC1 was correlated with many variables that had linear trends in time (Table 3). PC2 changed in a U-shaped fashion over time (Fig. 4) and reflected farming variables that were unimodal, including the number of sheep and the production of barley, most of which is spring sown (Fig. 5). Changes in applications of fertilizer and insecticides were also unimodal. PC3 was much more variable on a year-to-year basis than PC1 or PC2, but had an underlying unimodal shape. It correlated with some variables that showed strong unimodal trends (e.g. barley production; Table 3) but also with variables that were very noisy, for example rainfall in September of the previous year ($r = 0·647$, $P = 0·001$, $n = 22$) when the ground is normally prepared for winter crops. Hence PC3 may reflect some aspects of climatically driven variation in agriculture.

LINKING AGRICULTURAL CHANGE AND ARTHROPODS

We investigated links between agriculture and arthropods at three levels: the level of the raw data using average numbers per year; the level of the extracted trend; and by using PCA.

These different approaches gave broadly similar results (Table 4). The mean, median and standard deviation of the average catch per day per year for the 12 arthropod groups were significantly related to the previous year's values of agricultural PC1 and PC2. The mean, median and standard deviation of the GAM trends for the 12 groups indicated a significant relationship between arthropod abundance and current agriculture (agricultural PC1 and PC2), past agriculture (PC1 and PC3 in the previous year) and previous climate (NAO last year). Lastly, the three insect principal

time. Of all variables, PC3 was most strongly correlated with the previous autumn's rainfall and spring temperature. The association between PC3 and the arthropod groups correlated with it (e.g. Heteroptera, Psocoptera and Lepidoptera) perhaps indicates susceptibility to climate over the winter.

Table 2. Correlates of the PC axes from an analysis of the abundance of 12 arthropod groups from the suction trap (between 1972 and 1997). Variables are indicated when correlation has $P < 0·01$

|	Negative correlation	Positive correlation
PC1	Numbers of flies, Nematocera	Heteroptera, beetles, Psocoptera, Lepidoptera, Hymenotera, Thysanoptera, spiders, staphylinid beetles, weevils, median catch (per day per year per 'order'); July, August, September temperature, rainfall in previous autumn and winter
PC2	Carabid beetles; NHA	Mean numbers of insects (per day per year per order), SD insects, Collembola, flies (in total and three suborders individually), Homoptera, Neuroptera, Plecoptera, Trichoptera, mites
PC3	Heteroptera, Psocoptera, Ephemeroptera, Brachycera; January, February, March temperature	Lepidoptera; previous October–December rainfall
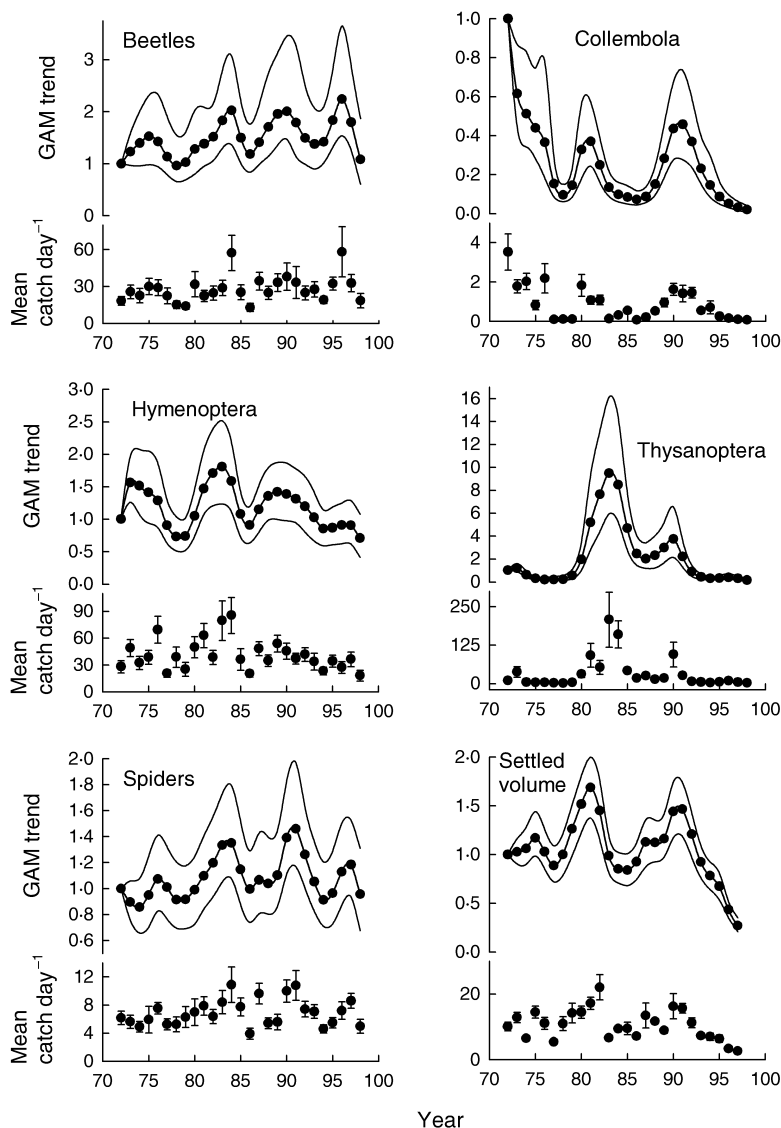
Fig. 3. Suction trap catches for 15 arthropod groups over 27 years were analysed to model the trends in numbers over the years, and examples are given to show the variability over time. For each group, the figure shows the extracted GAM trend, and the data (mean ± SE) catch per day per year. The GAM model was 12 d.f. for the year effect in each case, and 6 d.f. for the day effect for beetles, Hymenoptera, spiders and Thysanoptera, and 9 d.f. for Collembola and the settled volume of insects.

Table 3. The PC axes from an analysis of eight farming variables (from 1972 to 1997) are correlated with other measures of agriculture for the same period (see the Methods for sources of data). Variables are indicated when correlation has $P < 0.01$

	Negative correlation	Positive correlation
PC1	Area of crops and grass; area of rough grazing; loss of agricultural land; number of workers (full-, part-time or casual); area of barley and oats; amount of spring sown cereal	Head of cattle and sheep; number of poultry; area of wheat and rape; yield (per tonne) of barley, oat and wheat; amount of N, P or K fertilizer applied; value of NHA; year; size of total or agricultural economy
PC2	Area and production of barley; amount of lime applied; total cereal production; total fertilizer applied; amount of spring sown cereal	Number of part-time workers; number of pigs
PC3	Number of poultry; amount of P fertilizer; loss of agricultural land	Area and production of barley

components (PCs) were related to the agricultural PCs (PC1 in current year, PC1 and PC3 in the previous year) as well as the NAO in the previous year. Hence, although the details differed, each analysis revealed

links between arthropod abundance and agriculture (either the previous year, or current and previous year). The negative relationships between measures of arthropod numbers and the first two agricultural PC were of
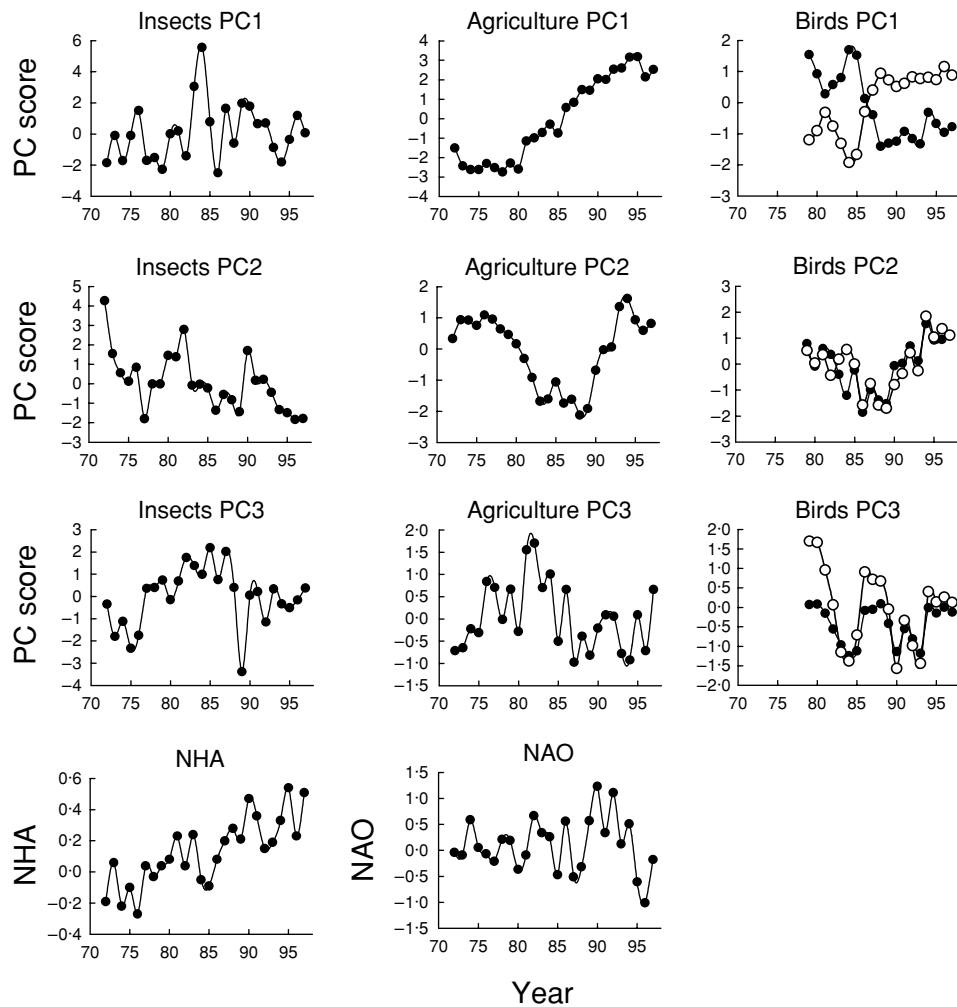
Fig. 4. The annual PC scores for the first three PCs extracted to 'summarize' the multivariate data for insects, agriculture and birds. The multivariate data used in the insect analysis was the average catch per year for the 12 common arthropod groups (whose median catch > 0). The agricultural data comprised eight representative time-series (such as shown in Fig. 5). The bird data comprised the average density per year averaged across Common Bird Census plots for the 15 common farmland bird species (those whose median density > 0). The Common Bird Census data suffer from particularly small sample sizes and geographical bias before 1979, so two PCAs were conducted. In the first analysis all data were included (filled circles), in the second only data from 1979 was included (open circles). There is strong correlation between the PC scores indicating that reducing the ratio of variables to data does not radically affect the PC scores. Also shown are two summary climatic variables: the annual northern hemisphere's temperature anomalies (NHA) and the annual values of the North Atlantic oscillation (NAO).

particular note, and indicated that there were more arthropods when farming was less intense, and when there were large areas of land producing cereal, predominantly spring-sown barley.

PATTERNS OF CHANGE IN BIRDS

There was considerable variation in the numbers of birds of the 15 most common species on the Common Birds Census plots from 1979 onwards (Fig. 6), but the variation between species was consistent. PCs extracted from the two analyses with data, respectively, from 1972 onwards and 1979 were strongly correlated (PC1 $r = -0.952$; PC2 $r = 0.839$; PC3 $r = 0.918$), despite small sample sizes and geographical bias in the early period. Hence, the PC scores seemed relatively robust.

The bird PCA from 1979 to 1997 extracted three components that accounted for 69% of the total vari-

ation (41%, 17%, 11%, respectively, for PC1–3; Fig. 5). PC1 was negatively correlated, in decreasing order of association, with chaffinch, yellowhammer, partridge, dunnock, robin and lapwing, and positively correlated with wren, crow, oystercatcher, swallow, skylark and NHA. PC2 was negatively correlated with skylark, starling, greenfinch and lapwing, and positively with oystercatcher and robin. PC3 was negatively correlated with linnet, dunnock, swallow, wren and robin, and positively with lapwing densities. It also reflected the mean and median densities across species and NAO in the previous year.

LINKING THE PATTERNS OF CHANGE IN FARMING, INSECTS AND BIRDS

We assessed associations between measures of bird abundance, whether the descriptive statistics of
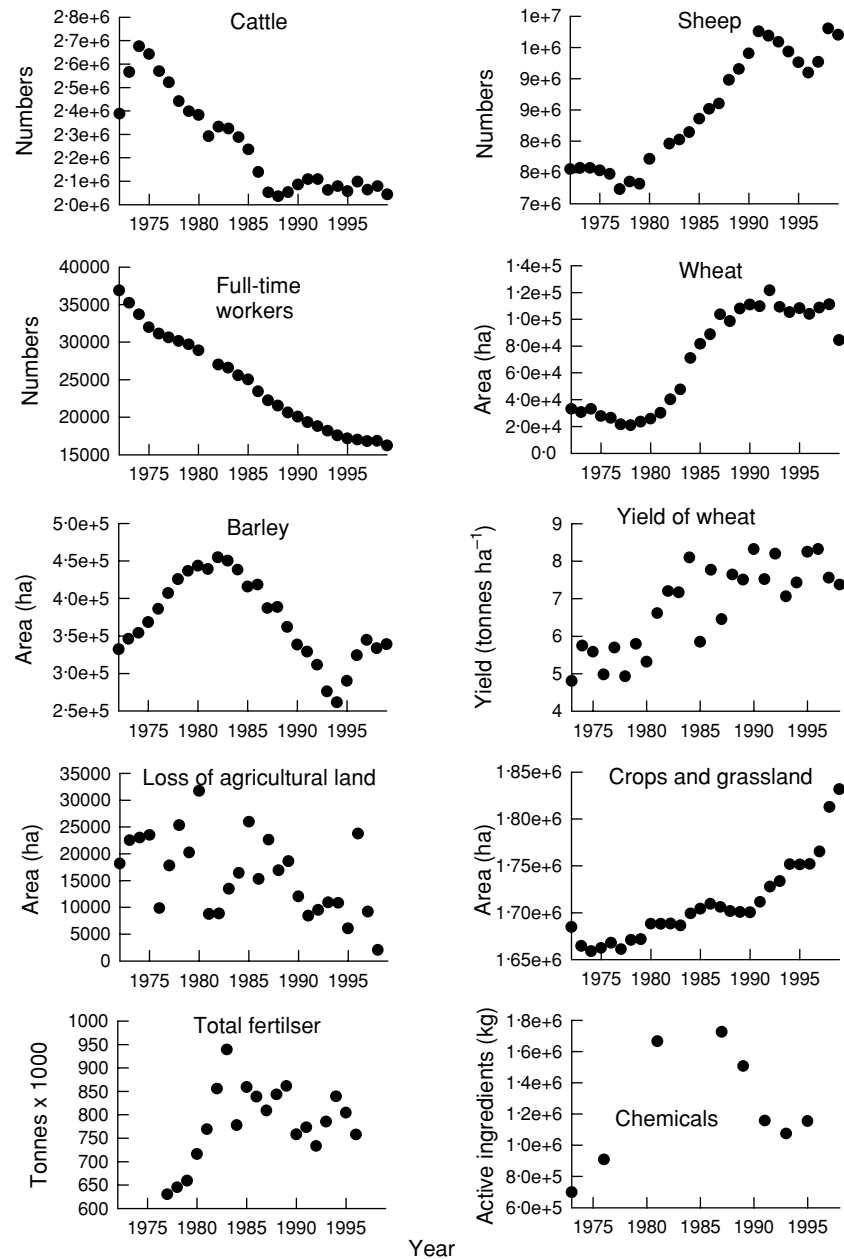
Fig. 5. Representative time-series of agricultural data for Scotland over the period of the study. The 'total fertilizer' is the sum of N, P, K fertilizers plus lime spread in Scotland. The 'chemicals' is the sum of the amount of active ingredient of all pesticides and growth regulators. The reduction in the weight of chemical application since the 1980s largely reflects change in the activity of the chemicals rather than a reduction in chemical usage, hence this variable describes agrochemical research as well as pesticide usage.

numbers or the PC scores, and measures of climate, and measures of farming practice (the PC scores) and measures of arthropods, whether descriptive statistics or PC scores. The results from different analyses differed quantitatively, but not qualitatively (Table 5): bird numbers reflected the measures of agriculture in the current and previous year, measures of arthropod numbers in the current year or in the current and previous year, depending on the analyses, and the climate. Analyses using the raw descriptive statistics of the bird and insect numbers or the PC scores both showed a relationship between birds and insects at time t and at $t − 1$. However, the effect of insects at time $t − 1$ was stronger in the analysis based on PC

scores, probably because by calculating PCA scores noise has been excluded, making the analysis more powerful.

In general, birds were more abundant in years, or following years, when there were more arthropods. Independently, birds were more abundant in years when agriculture was less intense (especially if the previous year had high rates of cereal planting, hence spring sowing). The analyses using the bird PC scores were more complicated to interpret (Fig. 7). The analysis using bird PC1 suggested that there were more chaffinches, yellowhammers and partridges, and fewer wrens and crows in years, or following years, with many arthropods and with low intensity farming. The bird

Table 4. Models of statistical association between agriculture and arthropods. Arthropod numbers (response variables) were measured as (a) the PC scores for the three PCs; (b) the average, median and SD of the annual values of the insect trends from the GAM models for the 12 common insect groups; or (c) the mean, median and SD of the average numbers of the 12 common insect groups (numbers per trap day per year). All models started with the main effects variables: agricultural PC1–3 (ag PC1–ag PC3), NHA and NAO at time = t, and also offset at time $t = -1$. The best univariate model was selected by Minitab's 'best subsets regression', which selects models based on maximizing R^2 and/or minimizing AIC. The MANOVA model included all variables initially and was simplified until all variables remaining were significant

Response variables	Variables in best model (CV, SE, P)	R^2 (adjusted)	Model P
(a) Response variables are yearly arthropod PC scores			
Insect PC1	ag PC2$_{t-1}$ (−0·88, 0·28, 0·005)	29	0·0005
Insect PC2	ag PC1$_t$ (−0·35, 0·12, 0·005), NAO$_t$ (0·88, 0·50, 0·09)	34	0·009
Insect PC3	ag PC1$_t$ (1·04, 0·35, 0·008), ag PC1$_{t-1}$ (−0·97, 0·36, 0·013),		0·002
	ag PC3$_{t-1}$ (1·10, 0·25, 0·000), NAO$_t$ (−0·90, 0·41, 0·041)	46	
MANOVA: insect PC1–3	ag PC1$_t$ ($F_{3,19}$ = 4·158, P = 0·020), ag PC2$_{t-1}$ ($F_{3,19}$ = 4·23, P = 0·019),		
	ag PC3$_{t-1}$ ($F_{3,19}$ = 4·79, P = 0·012), NAO$_t$ ($F_{3,19}$ = 3·49, P = 0·036)		
(b) Response variables are yearly summary statistics for catch per day across 12 common arthropod groups			
Mean	ag PC1$_{t-1}$ (−4·95, 2·20, 0·035), ag PC3$_{t-1}$ (9·6, 5·82, 0·113)	22	0·023
SD	ag PC1$_{t-1}$ (−15·94, 4·63, 0·002)	30	0·002
Median	ag PC1$_t$ (−0·59, 0·33, 0·086), ag PC3$_t$ (−0·84, 0·53, 0·129),		< 0·0005
	ag PC2$_{t-1}$ (−2·14, 0·40, 0·000), NHA$_{t-1}$ (8·49, 3·37, 0·020)	57	
MANOVA: mean,	ag PC1$_{t-1}$ ($F_{3,21}$ = 3·97, P = 0·022),		
median and SD	ag PC2$_{t-1}$ ($F_{3,21}$ = 7·90, P = 0·001)		
(c) Response variables are yearly summary statistics for GAM trends across 12 common arthropod groups			
Mean	ag PC2$_t$ (−0·27, 0·04, < 0·0005), NAO$_{t-1}$ (0·18, 0·08, 0·035)	69	< 0·0005
SD	ag PC2$_t$ (−0·39, 0·07, < 0·0005), ag PC3$_{t-1}$ (0·25, 0·08, 0·008)	73	< 0·0005
Median	ag PC2$_t$ (−0·14, 0·025, < 0·0005),		< 0·0005
	NAO$_{t-1}$ (0·13, 0·06, 0·03)	55	
MANOVA: mean,	ag PC2$_t$ ($F_{3,21}$ = 15·4, P < 0·0005),		
median and SD trend	ag PC3$_{t-1}$ ($F_{3,21}$ = 5·07, P = 0·009)		
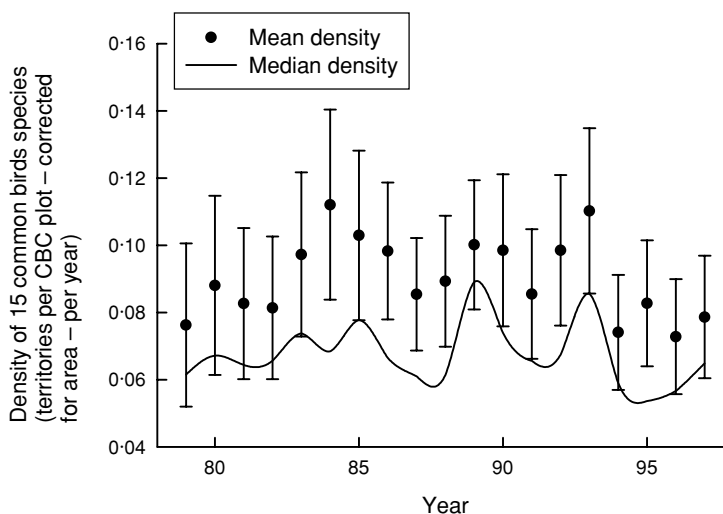
Fig. 6. Raw descriptive statistics showing the density of the 15 common species of bird since 1979 in Scotland. Error bars are SE. CBC, Common Bird Census.

PC2 analysis suggested there were more skylarks, starlings, greenfinches and lapwings when cereal production was high and insect numbers (PC1) were low. Bird PC3 suggested that the average number of birds in the Common Bird Census plots was positively associated with insect numbers but negatively with farming intensity.

Discussion

This study identifies temporal trends in a variety of arthropod groups and explores associations between farming, arthropods and birds. Multivariate measures of arthropod numbers were associated with multivariate measures of farming practice in the current and previous

Table 5. Models of the statistical influences of agriculture, arthropod and climate on bird numbers. Bird numbers (the response variables) were measured as (a) the mean, median and SD of the average numbers of the 15 common insect groups (territories per hectare per Common Bird Census plot per year), and (b) the PCs scores for the three PCs. Each analysis compared bird variable(s) with insect variables, agricultural variables and climatic variables at time t and $t - 1$, weighted by the number of Common Bird Census plots in each year. The insect variables for analysis (a) were the mean, median and SD (mean ins, med ins and SD ins) of the catches per group per day per year, and for (b) were the PC scores for the three PCs (ins PC1–ins PC3). The agricultural variables were the PC scores for the agricultural PCs (ag PC1– agPC3). The climatic variables were the annual NHA and NAO scores. The best univariate model was selected by Minitab's 'best subsets regression' which selects models based on both maximizing R^2 and minimizing AIC. The MANOVA model included all variables initially and was simplified until all variables remaining were significant

Response variables	Variables in best model (CV, SE, P)	R^2 (adjusted)	Model P
(a) Response variables are yearly bird counts averaged across 15 common species			
Mean	med Ins$_t$ (0·003, 0·001, 0·017), med Ins$_{t-1}$ (0·002, 0·001, 0·040), NHA$_{t-1}$ (−0·029, 0·012, 0·030)	45	0·007
Median	med Ins$_t$ (0·003, 0·001, 0·018), SD Ins$_{t-1}$ (0·0002, 0·00005, 0·007), ag PC1$_t$ (−0·012, 0·005, 0·030), ag PC2$_t$ (0·011, 0·003, 0·004), ag PC3$_t$ (0·011, 0·004, 0·015), ag PC1$_{t-1}$ (0·020, 0·006, 0·011), ag PC2$_{t-1}$ (−0·014, 0·003, 0·003), ag PC3$_{t-1}$ (−0·009, 0·004, 0·044), NHA$_t$ (−0·038, 0·014, 0·028), NHA$_{t-1}$ (−0·063, 0·018, 0·007)	68	0·017
SD	med Ins$_{t-1}$ (0·0016, 0·001, 0·130), ag PC1$_t$ (−0·005, 0·001, 0·001), NAO$_{t-1}$ (0·007, 0·004, 0·057)	53	0·002
MANOVA: bird mean, median and SD	mean Ins$_t$ ($F_{3,10}$ = 5·3, P = 0·019), SD ins$_t$ ($F_{3,10}$ = 5·8, P = 0·014), ag PC1$_t$ ($F_{3,10}$ = 25·9, P < 0·0005), ag PC2$_{t-1}$ ($F_{3,10}$ = 21·8, P < 0·0005), ag PC3$_{t-1}$ ($F_{3,10}$ = 5·2, P = 0·020), NHA$_t$ ($F_{3,19}$ = 4·1, P = 0·038)		
(b) Response variables are PCA scores from 1979+ analysis for 15 common bird species			
PC1	ins PC1$_t$ (−0·150, 0·055, 0·018), ins PC1$_{t-1}$ (−0·22, 0·049, 0·001), ag PC1$_t$ (0·316, 0·064, 0·000), ag PC2$_t$ (0·459, 0·200, 0·039), ag PC2$_{t-1}$ (−0·667, 0·209, 0·009), NHA$_{t-1}$ (2·088, 0·695, 0·012), NAO$_{t-1}$ (−0·453, 0·161, 0·017)	90	< 0·0005
PC2	ins PC1$_t$ (0·247, 0·056, 0·000), ins PC1$_{t-1}$ (0·139, 0·054, 0·014), ag PC2$_{t-1}$ (0·977, 0·103, 0·000)	83	< 0·0005
PC3	ins PC1$_t$ (−0·318, 0·043, 0·000), ins PC2$_{t-1}$ (−0·362, 0·080, 0·001), ins PC3$_{t-1}$ (0·371, 0·090, 0·002), ag PC3$_t$ (−0·552, 0·133, 0·002), ag PC1$_{t-1}$ (−0·754, 0·089, 0·000), NHA$_t$ (2·92, 0·629, 0·001), NHA$_{t-1}$ (4·16, 0·763, 0·000)	88	< 0·0005
MANOVA: PC1–3	ins PC1$_t$ ($F_{3,11}$ = 12·2, P = 0·001), ins PC1$_{t-1}$ ($F_{3,11}$ = 5·8, P = 0·013), ag PC1$_t$ ($F_{3,11}$ = 16·5, P < 0·0005), ag PC2$_{t-1}$ ($F_{3,11}$ = 27·5, P < 0·0005), NHA$_{t-1}$ ($F_{3,11}$ = 2·7, P = 0·095)		

years, as well as a summary measure of climate (the NAO) (Table 4). Likewise, multivariate measures of bird numbers were related to measures of current and past arthropod abundance and, independently, current and recent agriculture and climate (Table 5). Although correlative, these analyses support the view that changes in farming practice are linked to changes in bird populations over time. In particular, the data are consistent with the view that long-term intensification of agriculture affects farmland bird populations (Chamberlain *et al.* 2000), mediated through food availability (Vickery *et al.* 2001). The link between arthropods and bird populations in the following year is one that would be expected if arthropod availability influenced bird populations via breeding success or post-breeding and over-winter survival.

Our results (Tables 4 and 5 and Fig. 7) are generally in agreement with our predictions. When farming was more intense, there tended to be fewer arthropods. Bird numbers in turn were positively related to arthropod numbers, and negatively to many measures of farming intensity. As we would expect, there were often statistically significant lags in the association: the environmental state in the previous year impacted the bird numbers in the next year. The only association counter to expectation is shown in Fig. 7c: bird PC2 was correlated with higher values of insect PC1, and, independently, agricultural PC2. Lower values of agricultural PC2 were associated with greater cereal production, lower values of arthropod PC1 were associated with fewer insects, and lower values of bird PC2 were related to more skylarks, starlings, greenfinches and lapwings. That skylark numbers may be related to cereal production, predominantly spring-sown barley, is not surprising, but there appears to be an independent negative relationship between bird numbers and insect numbers. Controlling for area of cereal, this group of birds does better in years when insect numbers are lower. This could be causal, or there could be a confounding variable that might reduce total arthropod abundance but increase its availability by, for example, affecting vegetation structure.
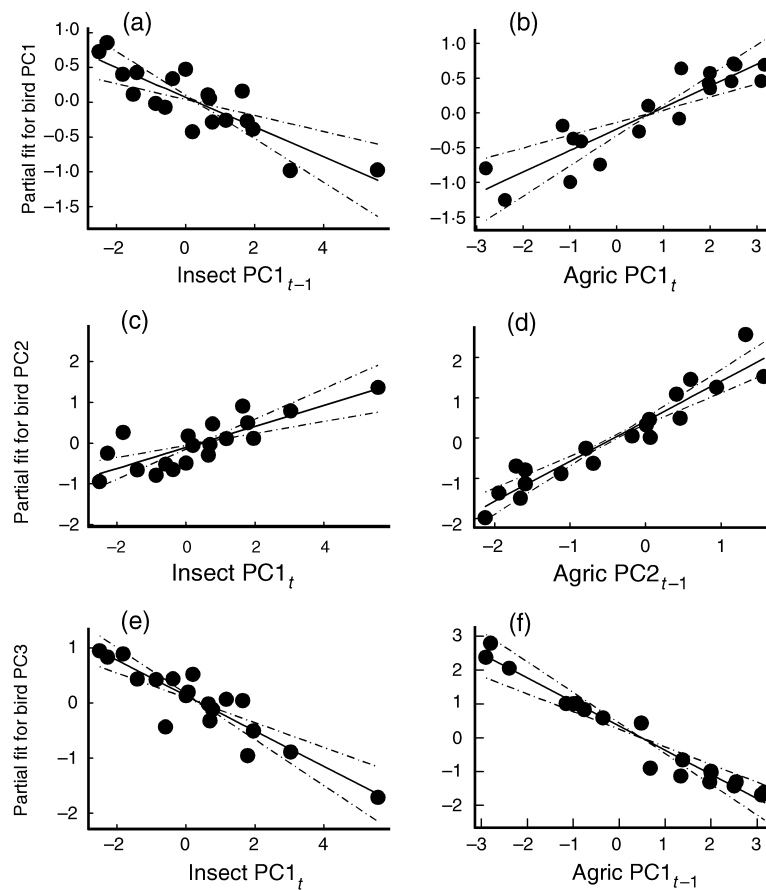
Fig. 7. The PCs from the analyses of bird densities are related to measures of insect abundance and agricultural practice. The partial fits and residuals from the models in Table 5 (i.e. controlling for the variation introduced by the other variables) were calculated for the two variables with the most significant relationships. The solid line shows the partial fits, the dotted line shows the SE of the fit and the dots show the 'partial data' (i.e. fit + residual). Bird PC1 and (a) insect PC1 at time $t − 1$ and (b) agricultural PC1 at time t; bird PC2 and (c) insect PC1 at time t and (d) agricultural PC2 at time $t − 1$; bird PC3 and (e) insect PC1 at time t and (f) agricultural PC1 at time $t − 1$.

Our study suggests that changes in arthropod abundances captured by a suction trap are related to regional changes in farming practice. The possible mechanisms that could link farming and insect populations are well documented. For example, organic fields tend to have more chick-food insects for partridges than paired conventional fields (Moreby & Sotherton 1997). Pesticides reduced insect numbers in unsprayed headlands (Sotherton 1991; de Snoo 1999), in subfield experiments (Moreby, Sotherton & Jepson 1997), and in a range of field-scale experiments (Holland *et al*. 1994). Intensification has often led to a reduction in area and quality of non-cropped habitat such as hedges, which are important sources of food and refugia for a range of plants and invertebrates (Dennis, Thomas & Sotherton 1994; Andersen 1997; Jonsen & Fahrig 1997; Cheeseman 1998; Fournier & Loreau 1999). The quality of grassland habitat has also changed (Vickery *et al*. 2001). Different crop types have different insect pests, but they are also likely to support different non-pest species. For example, oilseed rape harbours more insects compared with cereals (De Cornulier *et al*. 1997). Also, winter- and spring-sown cereals differ in their attractiveness to insects (Reddersen 1994). Therefore, changing patterns of farming, even within an intensive system, will lead to changes in insect populations.

Do these correlative patterns between birds and arthropods represent an underlying causality? Intensive single species studies have sometimes demonstrated the reliance of birds on insects. For example, grey partridge chick survival is related to insect abundance, particularly of their preferred prey, sawfly larvae (Southwood & Cross 1969; Green 1984). In unsprayed fields grey partridge raise larger broods with higher survival than in pesticide-sprayed fields (Rands 1986). In a number of hirundines, feeding rates, clutch size, laying dates, provisioning rates, chick growth rates and weights are related to suction trap catches (Bryant 1973, 1975; Turner 1980; Johnston 1990). Less detailed associations are known for some other species. For example, skylark broods are more likely to starve in intensively managed fields (Wilson *et al*. 1997). Chough *Pyrrhocorax pyrrhocorax* survival is thought to be related to invertebrate availability on farmland, which in turn is related to a field's previous agricultural history (McCracken & Foster 1994; McCracken & Bignal 1998; Laiolo & Rolando 1999). Lapwings feeding

in insect-rich areas lay larger eggs, after which chicks are moved by their parents to areas where insect density is high: chicks are more likely to die if they need to be moved farther to find insect-rich patches (Johansson & Blomqvist 1996; Blomqvist & Johansson 1995). Corn bunting foraging behaviour, chick growth and nest success are related to the abundance of chick-food insects, which, in turn, is related to pesticide usage (Brickle *et al.* 2000). Yellowhammers providing food for nestlings forage in a patchy habitat: if insect-rich patches become rarer, supply rates to young will decrease, leading to reduced productivity (Hinsley 2000; Morris *et al.* 2001).

This study supports the hypothesis that changes in bird numbers may be linked to changes in farming practice, at least in part through effects on farmland invertebrates. Two questions need to be addressed before we can suggest with any confidence that the relationships we have observed may be responsible for the UK-wide, or even Europe-wide, decline in birds. (i) Are data from a single suction trap sufficient to draw conclusions? (ii) Is Scotland broadly similar to elsewhere in the UK?

To take the first question, are data from a single suction trap sufficient to represent insect populations over the same geographical area covered by the farming and bird census data (broadly lowland Scotland)? Although suction traps sample aerial arthropods, they do correlate with abundance at ground level, at least in broad terms (Southwood 1960; Southwood & Cross 1969; Taylor 1974; Turner 1980). Taylor (1974) showed that the aerial distribution of insects was random, whereas the distribution of insects on the ground was clumped. Therefore, suction sampling was statistically more efficient than sampling at random within crops. Taylor (1974) also found that the numbers caught in paired suction traps on a given day were highly correlated, even with considerable distances between traps. For example, for aphids, at 1·7 m separation between traps: $r = 0·962$; at 1·4 km separation, $r = 0·921$; at 81 km separation, $r = 0·812$; and at 389 km separation, $r = 0·531$ (data from Taylor 1974; fig. 11 data from *c.* 400 days in each case). Similar patterns were found for single species through to whole orders. This suggests that a single trap is representative of a considerable geographical area (Taylor 1974): a 100-km radius is considered reasonable for aphid prediction purposes (I.P. Woiwod, personal communication). Within 100 km of Stirling can be found 52% of Scotland's arable land, and 64% of its livestock (data for 1996 from Snowden & McCreath 1997; *Economic Report on Scottish Agriculture* 1997). These figures suggest that, although our data come from a single trap, its catch is likely to correlate with the catch of any suction trap placed randomly in agricultural central Scotland. Incidentally, this implies that 12·2-m suction traps are useful tools for monitoring the biodiversity in the agricultural landscape in a quick and cost-effective way. Complete analysis of the catches of the already existing Rothamsted network of traps (Woiwod 1991) would provide important and

more detailed information about changes in farmland biodiversity than other existing monitoring tools.

With regard to the second question, are the associations found in the Scottish data generalizable to the UK overall, farmland birds have declined generally across the UK (Siriwardena *et al.* 1998) but the Scottish data suggest that long-term change in numbers is less marked than in England (Fig. 6). However, across all species there was a positive and significant correlation between the annual change in the BTO's index trends for the UK-wide data (which is biased towards data from south-east England) and changes in numbers in Scotland ($r = 0·284$, $P < 0·0005$, $n = 249$ from 15 species × *c.* 18 years), indicating that a high-density year for Scottish birds tends also to be a high-density year for birds in the whole UK. Moreover, the trends for individual species tend to be positively correlated (13 species were positively correlated, six significantly; six were negatively correlated, one significantly). Therefore there are broad similarities between both year-on-year changes in birds in Scotland and the UK, and their overall population dynamics. There are few comparative data for arthropods, but Aebischer (1991, fig. 15.5) reports on long-term sampling of insects in fields on five farms in southern England for the period 1972–89. During this period there was a general decline in arthropods (excluding mites and Collembola), with a regression slope of $-0·019 \pm 0·007$ log units of abundance per year. The Scottish data for the same period showed similar declines, with a regression slope of $-0·023 \pm 0·011$. Both slopes were different from zero but not significantly different from each other. As with the bird data, this implies that Scottish insects are likely to change in similar ways to those in England. Regional differences exist in farming practice, but these are much reduced from former years (driven by widely available technology, chemicals, legal and policy frameworks, including the European Union), so it is likely that farming practices change similarly across the UK as a whole. For example, at a broad scale our agricultural PC1 correlated highly significantly with the major axis of agricultural change shown by Chamberlain *et al.* (2000) based predominantly on data from England and Wales.

We therefore propose that associations between farming, insects and birds are potentially causal in nature, and also perhaps broadly applicable across the UK as a whole. If this is the case, then we predict that managing farming to maximize key insect populations will aid birds living on the farmland. Perhaps the most obvious way to do this is to increase the area of non-cropped habitat (such as wider, unsprayed, headlands or field margins, or set-aside). Given that foraging costs will be related to the travel costs to find food-rich patches, management that allows adjacent nesting and foraging habitat for birds would be especially beneficial. Freemark & Kirk (2001) found an association with local habitat heterogeneity and bird diversity, and suggest that a prime benefit of organic agriculture is the

associated increase in heterogeneity rather than a reduction in chemical application *per se*.

The new technology of genetically modified (GM) herbicide-tolerant crops may result in a reduction of non-crop plants (Watkinson *et al.* 2000). This may reduce the seeds available as winter food for farmland birds (Watkinson *et al.* 2000) but it is also likely to reduce further insect populations that breed on the non-crop plants. Our results imply that the possible impact of GM technology on insect populations, and therefore on the food available for birds during their breeding season, may become as significant as the reduction in seeds available.

Acknowledgements

References

Aebischer, N.J. (1991) Twenty years of monitoring invertebrates and weeds in cereal fields in Sussex. *The Ecology of Temperate Cereal Fields* (eds L.G. Firbank, N. Carter, J.F. Darbyshire & G.R. Potts), pp. 305–331. Blackwell Scientific Publications, Oxford, UK.

Andersen, A. (1997) Densities of overwintering carabids and staphylinids (Col., Carabidae and Staphylinidae) in cereal and grass fields and boundaries. *Journal of Applied Entomology*, **121**, 77–80.

Blaxter, K. & Robertson, N. (1995) *From Dearth to Plenty: The Second Agricultural Revolution*. Cambridge University Press, Cambridge, UK.

Blomqvist, D. & Johansson, O.C. (1995) Trade-offs in nest site selection in coastal populations of lapwings *Vanellus vanellus*. *Ibis*, **137**, 550–558.

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*. *Journal of Applied Ecology*, **37**, 742–755.

Bryant, D.M. (1973) The factors influencing the selection of food by the house martin (*Delichon urbica* L.). *Journal of Animal Ecology*, **42**, 539–564.

Bryant, D.M. (1975) Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. *Ibis*, **117**, 180–216.

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 No. 227. Joint Nature Conservation Committee, Peterborough, UK.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 771–788.

Cheeseman, O. (1998) The impact of some field boundary management practices on the development of *Dipsacus fullonum* L. flowering stems, and implications for conservation. *Agriculture, Ecosystems and the Environment*, **68**, 41–49.

De Cornulier, T., Bernard, R., Arroyo, B. & Bretagnolle, V. (1997) Geographic extension and change in the ecology of the bluethroat *Luscinia svecica* in central-western France. *Alauda*, **65**, 1–6.

Dennis, P., Thomas, M.B. & Sotherton, N.W. (1994) Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. *Journal of Applied Ecology*, **31**, 361–370.

Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology*, **81**, 1970–1984.

Fournier, E. & Loreau, M. (1999) Effects of newly planted hedges on ground beetle diversity (Coleoptera, Carabidae) in an agricultural landscape. *Ecography*, **22**, 87–97.

Freemark, K.E. & Kirk, D.A. (2001) Birds on organic and conventional farms in Ontario: partitioning effects of habitat and practices on species composition and abundance. *Biological Conservation*, **101**, 337–350.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D. & Carter, N. (1995) Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, **9**, 1425–1441.

Gardner, B. (1996) *European Agriculture: Policies, Production and Trade*. Routledge, London, UK.

Gillings, S. & Fuller, R.J. (1998) Changes in bird populations on sample lowland English farms in relation to loss of hedgerows and other non-crop habitats. *Oecologia*, **116**, 120–127.

Green, R.E. (1984) The feeding ecology and survival of partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in East Anglia. *Journal of Applied Ecology*, **21**, 817–830.

Harvey, G. (1997) *The Killing of the Countryside*. Vintage, London, UK.

Hastie, T.J. & Tibshirani, R.J. (1990) *Generalised Additive Models*. Chapman & Hall, London, UK.

Hinsley, S.A. (2000) The costs of multiple patch use by birds. *Landscape Ecology*, **15**, 765–775.

Holland, J.M., Frampton, G.K., Çilgi, T. & Wratten, S.D. (1994) Arable acronyms analysed – a review of integrated arable farming systems research in western Europe. *Annals of Applied Biology*, **125**, 399–438.

Holmes, J.C. (1995) Population regulation: a dynamic complex of interactions. *Wildlife Research*, **22**, 11–19.

James, F.C., McCulloch, C.E. & Wiedenfield, D.A. (1996) New approaches to the analysis of population trends in land birds. *Ecology*, **77**, 13–27.

Johansson, O.C. & Blomqvist, D. (1996) Habitat selection and diet of lapwing *Vanellus vanellus* chicks on coastal farmland in south-east Sweden. *Journal of Applied Ecology*, **33**, 1030–1040.

Johnston, R.D. (1990) *Effects of nestling diet quality on the growth and adult size of passerine birds*. Unpublished PhD Thesis. University of Stirling, Stirling, UK.

Jones, P.D., New, M., Parker, D.E., Martin, S. & Rigor, I.G. (1999) Surface air temperature and its changes over the past 150 years. *Reviews of Geophysics*, **37**, 173–199.

Jonsen, I.D. & Fahrig, L. (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecology*, **12**, 185–197.

Krebs, J.R., Wilson, J.D., Bradbury, R.M. & Siriwardena, G.M. (1999) The second silent spring? *Nature*, **400**, 611–612.

Laiolo, P. & Rolando, A. (1999) The diet of the chough (*Pyrrhocorax pyrrhocorax*) and the Alpine chough (*Pyrrhocorax graculus*) in the Alps: seasonality, resource partitioning and population density. *Revue D'ecologie – la Terre et la Vie*, **54**, 133–147.

Macaulay, E.D.M., Tatchell, G.M. & Taylor, L.R. (1988) The Rothamsted Insect Survey '12 metre' suction trap. *Bulletin of Entomological Research*, **78**, 121–129.

McCracken, D.I. & Bignal, E.M. (1998) Applying the results of ecological studies to land-use policies and practices. *Journal of Applied Ecology*, **35**, 961–967.

McCracken, D.I. & Foster, G.N. (1994) Invertebrates, cow dung and the availability of potential food for the chough (*Pyrrhocorax pyrrhocorax* L.) on pastures in North West Islay. *Environmental Conservation*, **21**, 262–266.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman & Hall, New York.

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

Moreby, S.J. & Sotherton, N.W. (1997) A comparison of some important chick-food insect groups found in organic and conventionally-grown winter wheat fields in southern England. *Entomological Research in Organic Agriculture*, **1997**, 51–60.

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. *Agriculture, Ecosystems and the Environment*, **72**, 285–297.

Moreby, S.J., Sotherton, N.W. & Jepson, P.C. (1997) The effects of pesticides on species of non-target Heteroptera inhabiting cereal fields in southern England. *Pesticide Science*, **51**, 39–48.

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*) nesting in agriculturally contrasting regions in lowland England. *Biological Conservation*, **101**, 197–210.

Osborn, T. (2000) *The North Atlantic Oscillation*. Information Sheet 11. Climatic Research Unit, University of East Anglia, Norwich, UK. http://www.cru.uea.ac.uk/cru/info/nao.

Payne, R.J.H. & Wilson, J.D. (1999) Resource limitation in seasonal environments. *Oikos*, **87**, 303–314.

Peach, W.J., Siriwardena, G.M. & Gregory, R.D. (1999) Long-term changes in over-winter survival rates explain the decline of reed buntings *Emberiza schoeniclus* in Britain. *Journal of Applied Ecology*, **36**, 798–811.

Rands, M.R.W. (1986) The survival of gamebird (Galliformes) chicks in relation to pesticide use in cereal fields. *Ibis*, **128**, 57–64.

Reddersen, J. (1994) Distribution and abundance of lauxaniid flies in Danish cereal fields in relation to pesticides, crop and field boundary (Diptera, Lauxaniidae). *Entomologiske Meddelelser*, **62**, 117–128.

Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. (1998) Trends in abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology*, **35**, 24–43.

Siriwardena, G.M., Baillie, S.R., Crick, H.P.Q. & Wilson, J.D. (2000) The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. *Journal of Applied Ecology*, **37**, 128–148.

de Snoo, G.R. (1999) Unsprayed field margins: effects on environment, biodiversity and agricultural practice. *Landscape and Urban Planning*, **46**, 151–160.

Snowden, J.P. & McCreath, M. (1997) *Pesticide Usage in Scotland: Arable Crops 1996*. Scottish Office Agriculture and Fisheries Department, Edinburgh, UK.

Sotherton, N.W. (1991) Conservation headlands: a practical combination of intensive cereal farming and conservation. *The Ecology of Temperate Cereal Fields* (eds L.G. Firbank, N. Carter, J.F. Darbyshire & G.R. Potts), pp. 373–397. Blackwell Scientific Publications, Oxford, UK.

Sotherton, N.W. (1998) Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. *Biological Conservation*, **83**, 259–268.

Southwood, T.R.E. (1960) The flight activity of Heteroptera. *Transactions of the Royal Entomological Society, London*, **112**, 173–220.

S-Plus (2000) *Guide to Statistics*, Vol. 1. Data analysis products Division, Mathsoft, Seattle, WA, USA.

Southwood, T.R.E. & Cross, D.J. (1969) The ecology of the partridge. III. Breeding success and the abundance of insects in natural habitats. *Journal of Animal Ecology*, **38**, 497–509.

Taylor, L.R. (1973) Monitoring change in the distribution and abundance of insects. *Report of the Rothamsted Experimental Station for 1973*, **2**, 202–239.

Turner, A.K. (1980) *The use of time and energy by aerial feeding birds*. Unpublished PhD Thesis. University of Stirling, Stirling, UK.

Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. & Brown, V.K. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, **38**, 647–664.

Watkinson, A.R., Freckleton, R.P., Robinson, R.A. & Sutherland, W.J. (2000) Predictions of biodiversity response to genetically modified herbicide-tolerant crops. *Science*, **289**, 1554–1557.

Wilson, J.D., Evans, J., Browne, S.J. & King, J.R. (1997) Territory distribution and breeding success of skylarks on organic and intensive farmland in southern England. *Journal of Applied Ecology*, **34**, 1462–1478.

Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C. & Bradbury, R.B. (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems and the Environment*, **75**, 13–30.

Woiwod, I.P. (1991) The ecological importance of long-term synoptic monitoring. *The Ecology of Temperate Cereal Fields* (eds L.G. Firbank, N. Carter, J.F. Darbyshire & G.R. Potts), pp. 275–304. Blackwell Scientific Publications, Oxford, UK.