

The demography of lowland farmland birds

GAVIN M. SIRIWARDENA^{1,2}, STEPHEN R. BAILLIE¹, HUMPHREY Q.P. CRICK¹,
JEREMY D. WILSON^{2#} & SIMON GATES^{1†}

¹ British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK

² Ecology and Behaviour Group, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK

[#] Current address: Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

[†] Current address: National Perinatal Epidemiology Unit, Radcliffe Infirmary, Woodstock Road, Oxford, OX2 6HE, UK

We review the results of a three-year investigation into the demography of lowland farmland bird population changes and its relationship with agriculture, using long-term data on abundance, annual survival rates, breeding productivity (per nesting attempt) and land-use, also considering the findings of other, related studies. We concentrated on 14 predominantly granivorous species, but considered a wider range of species for our analyses of abundance and survival data. Analysis of 42 species' population trends showed that declines were associated strongly with farmland specialists, but no large, clear groups of species were found to have closely similar long-term trends. Nevertheless, certain short periods have been associated with similar changes in trend direction across many species. These results suggest that a range of specific environmental causes are needed to explain population change across farmland bird species, but that particular environmental events could have had widespread impacts. However, species-specific demography and population processes may obscure the generality of some causes and mechanisms. Detailed analysis of changes in annual survival rate for six granivorous species showed that they have been sufficient to explain population changes only for Goldfinch *Carduelis carduelis* and House Sparrow *Passer domesticus*. However, analyses of average survival rate over blocks of years and evidence from other studies showed that changes in survival rate could have been an important mechanism behind population change for at least 13 of 28 farmland bird species. Changes in fledgling production per nesting attempt were consistent with important roles determining abundance for only one of twelve granivorous species (Linnet *Carduelis cannabina*). More commonly, fledgling production increased during periods of decline. A greater role for annual survival than for fledgling production per attempt in driving population changes seems to be general for declining nidicolous farmland birds, but changes in fledgling production could have been more important for nidifugous and increasing nidicolous species. It is important, to note, however, that we were unable to measure changes in post-fledging survival rates or the numbers of breeding attempts made in a season, which several sources of evidence indicate to have been important. Nevertheless, our analyses of the influences of agricultural land-use on fledgling production per attempt revealed several widespread positive effects of low-intensity agricultural practices (which have declined in recent years) such as mixed land-use, high crop diversity and the presence of fallow land. These occurred despite the paucity of detectable declines in the fledgling production of nidicolous farmland seed-eaters. These results show that relationships between habitat variables and fledgling production can be strong statistically but relatively unimportant in terms of ecological effect, and they have important implications for local and short-term studies. Future demographic work should focus on the environmental causes of changes in survival rates and on the causes and implications of changes in post-fledging survival rates and numbers of breeding attempts.

A number of the papers in these proceedings describe local, intensive investigations into the ecological mechanisms for and environmental causes of changes, principally declines, in the abundance of farmland birds. Such studies can reveal environmental correlates of variations in demographic parameters such as clutch size and nest failure rates and thus suggest causes and mechanisms for national population declines. They can be particularly strong when based on controlled comparisons of types of farmland habitat or management, which effectively form experimental designs. An alternative and complementary approach to elucidating the causes of population change

is to investigate historical national data on demographic rates. Through analyses of such data we can measure how demography has changed and construct models to assess how well the changes explain past population trends. We can also integrate historical land-use data with demographic data to investigate the environmental causes of population changes. This approach suffers in comparison with intensive work in that it is dependent on data that have not usually been collected with the current analytical goal in mind, so supporting information (such as that on habitat) and data quality may not be ideal. However, it is not limited to local study sites and considers

the national (or at least larger-scale) populations that actually underwent the changes of interest, rather than birds living long after the changes occurred.

The Common Birds Census (CBC) of the British Trust for Ornithology (BTO) provided the first evidence of severe declines in British lowland farmland bird populations in the 1970s and 1980s (O'Connor & Shrubbs 1986, Marchant *et al.* 1990, Fuller *et al.* 1995). Many species were affected including, notably, a range of predominantly granivorous species. Together with other national long-term data sets held by the BTO, the CBC provides a historical context within which farmland bird demography can be investigated (Table 1, Baillie 1990). Each source of demographic data has strengths and weaknesses related to the scale and method of data collection, and these are summarised in Table 1. Historical data are available for

most of the key demographic parameters, such as survival rates, nest success and clutch size, but reliable information on numbers of breeding attempts and on survival rates over the period immediately after fledging is lacking.

In this paper we review the findings of a three-year investigation of the relationships between trends in farmland bird abundance, demographic rates and agricultural land-use using BTO data sets. Commonalities across species in population trends or demographic relationships would suggest, in conjunction with the ecological characteristics of the species concerned, where similar effects of the environment have occurred on different species' populations. Agricultural land-use data were obtained from national agricultural censuses. Our analyses concentrated on a set of fourteen broadly granivorous farmland bird species which have undergone

Table 1. Summary of the available sources of data on various demographic parameters for British lowland farmland birds, considering the strengths and weaknesses of each.

Data source	Demographic parameters available	Strengths and weaknesses
Common Birds Census ¹	Abundance relative to an index year ²	Long, national time-series for southern Britain can be related to other demographic data. Survey plot sample is non-random but representative of lowland farmland in much of Britain (Fuller <i>et al.</i> 1985).
Ring-recoveries from the national Ringing Scheme	Annual adult, first-year and (potentially) post-fledging survival rates ²	Long national time-series can be related to other demographic data. Falling reporting rates (not currently estimable) may bias survival-rate estimates for longer-lived species. Habitat coverage is non-random and farmland may be under-sampled.
Nest Records Scheme	Fledgling production per nesting attempt and its component demographic parameters (such as clutch size and daily failure rates) ²	Long national time-series (Crick & Baillie 1996) can be related to other demographic data. Detailed habitat data available. Readily spatially referenced. Sampling is non-random and dependent on observer choice. Late-season nests are under-sampled. No data on number of breeding attempts or on period between fledging and independence.
Constant Effort Sites	Annual adult survival rates, abundance and productivity indices for a restricted range of species (Peach 1993)	Not based in farmland habitats and established after the principal population changes occurred. Changes in rates of emigration from sites would cause biases.
Retrapping Adults for Survival	Annual adult survival rates for selected species (Baillie 1996)	Scheme began in 1998, so little useful information available as yet (Balmer 1999).
Intensive Field Studies	Potentially, breeding success (including numbers of breeding attempts), annual survival and post-fledging survival rates.	Can be tightly focused to address specific questions. Data collection (by professionals) can be complex and well standardized. Are necessarily local and limited in geographical extent so cannot be generalized to the national scale. If short-term, are limited to contemporary populations that may not be representative of those that underwent changes in abundance in the past unless analogous historical data are available. Estimates of survival rates can be biased by emigration from study areas and studies are often too short-lived to generate good survival data.

1. Further, (conceptually) equivalent, but less biased, data are available from 1994 onwards from the Breeding Bird Survey.

2. These data can be combined to produce an estimate of the combined influence of variation in the number of breeding attempts and post-fledging survival rates on abundance (Siriwardena *et al.* 2000a).

a range of long-term trends in abundance: Grey Partridge *Perdix perdix*, Turtle Dove *Streptopelia turtur*, Tree Sparrow *Passer montanus*, House Sparrow, *P. domesticus*, Skylark *Alauda arvensis*, Linnet *Carduelis cannabina*, Bullfinch *Pyrrhula pyrrhula*, Yellowhammer *Emberiza citrinella* and Corn Bunting *Miliaria calandra* (all, broadly, declining); Stock Dove *Columba oenas* and Chaffinch *Fringilla coelebs*

(increasing); Greenfinch *Carduelis chloris*, Goldfinch *C. carduelis* and Reed Bunting *Emberiza schoeniclus* (stable in the long term, but Goldfinch and, especially, Reed Bunting have also undergone periods of decline). This list was expanded to include as many farmland species as possible when it was straightforward and informative to do so (in our analyses of CBC trends and of survival rates).

Table 2. Changes in the smoothed Mountford index of abundance for 1968-1995 for 42 bird species found on farmland. Species in bold are farmland specialists (see Siriwardena *et al.* 1998a, from which this table is adapted). Changes shown in bold are significant (confidence intervals do not include 1.00). Confidence intervals were obtained by bootstrapping: no interval is given where the data were too sparse to allow meaningful confidence intervals to be calculated. The average population change for farmland specialists was significantly more negative than that for generalist species ($P < 0.01$: see Siriwardena *et al.* 1998a).

Species	1995 index value as proportion of 1968 one	95% confidence interval
Tree Sparrow <i>Passer montanus</i>	0.17	0.03 - 0.95
Grey Partridge <i>Perdix perdix</i>	0.26	0.14 - 0.48
Turtle Dove <i>Streptopelia turtur</i>	0.35	-
Song Thrush <i>Turdus philomelos</i>	0.37	0.28 - 0.47
Sedge Warbler <i>Acrocephalus schoenobaenus</i>	0.38	-
Corn Bunting <i>Miliaria calandra</i>	0.39	-
Skylark <i>Alauda arvensis</i>	0.51	0.42 - 0.63
Garden Warbler <i>Sylvia borin</i>	0.52	0.12 - 1.95
Mistle Thrush <i>Turdus viscivorus</i>	0.53	0.39 - 0.72
Bullfinch <i>Pyrrhula pyrrhula</i>	0.55	0.25 - 0.90
Linnet <i>Carduelis cannabina</i>	0.59	0.41 - 0.87
Blackbird <i>Turdus merula</i>	0.59	0.50 - 0.67
Starling <i>Sturnus vulgaris</i>	0.60	0.39 - 0.89
Whitethroat <i>Sylvia communis</i>	0.62	0.42 - 0.85
Lapwing <i>Vanellus vanellus</i>	0.62	0.20 - 3.40
Dunnock <i>Prunella modularis</i>	0.67	0.52 - 0.81
Reed Bunting <i>Emberiza schoeniclus</i>	0.73	0.40 - 1.27
Yellowhammer <i>Emberiza citrinella</i>	0.74	0.58 - 0.94
Willow Warbler <i>Phylloscopus trochilus</i>	0.78	0.60 - 1.03
Red-legged Partridge <i>Alectoris rufa</i>	0.87	-
Treecreeper <i>Certhia familiaris</i>	0.91	-
Swallow <i>Hirundo rustica</i>	0.97	0.66 - 1.41
Chiffchaff <i>Phylloscopus collybita</i>	0.98	0.66 - 1.57
Greenfinch <i>Carduelis chloris</i>	1.03	0.77 - 1.48
Moorhen <i>Gallinula chloropus</i>	1.04	0.67 - 1.42
Lesser Whitethroat <i>Sylvia curruca</i>	1.09	0.44 - 2.87
Cuckoo <i>Cuculus canorus</i>	1.17	0.79 - 1.62
Chaffinch <i>Fringilla coelebs</i>	1.28	1.11 - 1.48
Blue Tit <i>Parus caeruleus</i>	1.33	1.08 - 1.49
Robin <i>Erithacus rubecula</i>	1.35	1.13 - 1.53
Goldfinch <i>Carduelis carduelis</i>	1.59	1.08 - 2.30
Jackdaw <i>Corvus monedula</i>	1.60	-
Pied Wagtail <i>Motacilla alba</i>	1.64	1.15 - 2.41
Great Tit <i>Parus major</i>	1.78	1.45 - 2.12
Magpie <i>Pica pica</i>	1.83	1.48 - 2.25
Pheasant <i>Phasianus colchicus</i>	1.87	1.06 - 2.79
Wren <i>Troglodytes troglodytes</i>	1.99	1.68 - 2.28
Carrion Crow <i>Corvus corone</i>	2.15	1.62 - 2.81
Blackcap <i>Sylvia atricapilla</i>	2.20	1.58 - 3.20
Mallard <i>Anas platyrhynchos</i>	2.31	1.52 - 3.05
Long-tailed Tit <i>Aegithalos caudatus</i>	2.32	1.50 - 4.09
Stock Dove <i>Columba oenas</i>	2.62	1.42 - 5.91

LONG-TERM TRENDS IN ABUNDANCE

Although much of the concern about the conservation status of farmland birds in Britain initially derived from trends in CBC indices (O'Connor & Shrubbs 1986, Marchant *et al.* 1990), the trends and changes in abundance shown by the survey had not been quantified using a statistically rigorous method before the start of our study. The apparent similarities between the population trends undergone by large groups of species had also not been confirmed objectively. The habitat coverage of the CBC is representative of agricultural land-use in south and east Britain (Fuller *et al.* 1985), in which area survey plots are concentrated. The survey does not monitor populations elsewhere in Britain, so it includes no information on the extreme north-west, from where some species have retreated during their declines (Gibbons *et al.* 1993). CBC methodology is discussed in detail in Marchant *et al.* (1990).

We used recently developed techniques for the analysis of annual count data, which minimise the statistical problems that can afflict older methods of population

index calculation (Mountford 1982, 1985, Peach & Baillie 1994) to quantify changes in the farmland CBC indices of 42 species between 1968 and 1995. We then applied a non-parametric smoothing algorithm to identify long-term trends and to separate them from the “noise” of annual fluctuations and sampling error (Siriwardena *et al.* 1998a). The results showed that most of the declines identified previously can be considered to be both robust and statistically significant (a notable exception was Swallow *Hirundo rustica*, for which the evidence for a decline was found to be weak) (Table 2). Analyses using generalised additive models provided further confirmation of the population changes undergone by seed-eating farmland birds (Fewster *et al.* 2000). In addition, when we investigated whether a number of ecological and phylogenetic classifications were good predictors of population change across species, only one was significant: species that specialise on farmland in Britain have declined much more, on average, than habitat generalists (30% decline versus 23% increase: Table 2, Siriwardena *et al.* 1998a; other categorisations and variables tested included diet, nesting strategy, migration strategy, body length and clutch size).

Table 3. Groups of species with similar smooth long-term farmland CBC trends identified quantitatively from a measure of the dissimilarity between the trends of 42 species (several species did not fall into clear groups) (Siriwardena *et al.* 1998a) and summaries of the possible implications of the trends.

Group of species	Summary of trend shown	Possible implications
Blackbird Mistle Thrush Song Thrush Skylark	Declining, especially from mid-1970s.	Common environmental and demographic mechanisms, reflecting similar behaviour, diet and habitat, especially for the thrushes.
Great Tit Blue Tit	Slight increases fluctuating in parallel.	Common environmental and demographic mechanisms, reflecting similar behaviour, diet and habitat.
Wren Long-tailed Tit Pied Wagtail	Increasing in the long term with a peak in abundance in the mid-1970s followed by a crash and a period of stability.	Common environmental and demographic mechanisms, reflecting similar resident insectivorous strategy.
Whitethroat Willow Warbler Garden Warbler	Common patterns of decline in the early 1970s followed by stability and subsequent recovery.	Common environmental and demographic mechanisms, reflecting similar migrant behaviour (winter conditions)*.
Mallard Magpie Carrion Crow Blackcap Chaffinch Stock Dove	Smooth steady increases.	Species that are generalist or incidental on farmland, probably increasing for several different reasons. Most commensal with humans or adept at exploiting anthropogenic food sources.
Reed Bunting Red-legged Partridge	Stable in the long term with a transient peak in abundance in the mid- to late 1970s.	Coincidental trends due to species-specific factors.

* Similarities were also apparent between the trends of these species and those of Chiffchaff and Sedge Warbler in the early 1970s.

To investigate in more detail whether species had shared common long-term population trends, we compared their smoothed CBC index series objectively and quantitatively (Siriwardena *et al.* 1998a). Using data from 1968 to 1995 (thus omitting the portions of trends that were heavily influenced by cold winters in the early 1960s), we transformed smoothed CBC trends to remove information on the rate of population change, leaving information only on trend direction and the timing of changes in direction. The area between these transformed index series was used as a measure of the dissimilarity between species' trends. Analyses considering the dissimilarities between the trends of all 42 species showed that large groups of species with closely similar long-term trends could not be found (Siriwardena *et al.* 1998a). This shows that species' trends tended to differ at least, in, the precise timing of changes in direction. Some small groups of species with common trend patterns were found, however, and some of these suggest the action of common environmental causes (Siriwardena *et al.* 1998a): see Table 3.

Although large numbers of species had not undergone closely similar population trends in the long term, it was still possible that common patterns had occurred within restricted periods, or with only small differences in timing across species. We investigated this by looking for turning points in smoothed CBC trends and comparing their timing across species. A turning point was defined as a year in which a point-estimate of the rate of change of the gradient (i.e. the second derivative) of a CBC trend at that time was statistically significantly different from zero (Siriwardena *et al.* 1998a). We found significant turning points within the index series of most of the species considered and the distribution of turning points across species with respect to time showed several clear clusters of both upturns and downturns (Fig. 1). This shows that particular periods have been associated with similar changes in the population trends of a range of species, suggesting that certain environmental events (or combinations of events) have each had a widespread impact across species. The pattern was the same for each group when declining and increasing/stable species were considered separately (Siriwardena *et al.* 1998a). Periods featuring downturns included the mid-1970s, previously cited as a key period in the declines of many farmland birds (Fuller *et al.* 1995) and the late 1960s, when the trends of many species levelled off after recovering from the effects of cold winters at the beginning of the decade. The group of downturns in the late 1980s (Fig. 1) showed the onset of a new set of declines, but many of these were reversed by upturns in 1992-1993 (Siriwardena *et al.* 1998a), which might indicate the positive effects of set-aside land. While the species showing such upturns were as diverse as Grey Partridge, Song Thrush *Turdus philomelos* and Wren *Troglodytes troglodytes*, recent work has found that

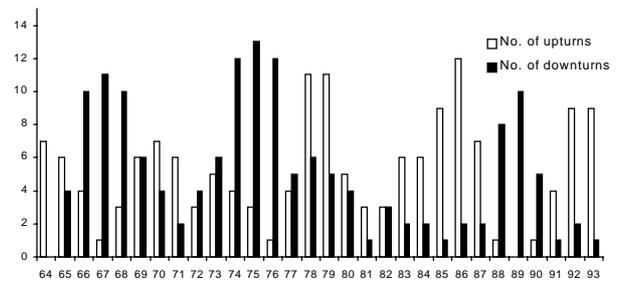


Figure 1. Graph of the occurrence across species of significantly non-zero values of second derivatives in each year, separated by sign. The value of the second derivative in a given year was taken to be significantly non-zero if the bootstrapped 95% confidence interval for that value did not overlap zero. Positive second derivatives represent points where a species' smoothed Mounford index series curve was turning up, and negative values where it was turning down. Adapted from Siriwardena *et al.* (1998a).

species in almost all foraging guilds using farmland (excepting only corvids) show clear preferences for set-aside (Henderson & Evans 2000, Henderson *et al.* 2000, in press) suggesting that it could have benefited many species. Earlier sets of upturns may best be interpreted as the levelling off of periods of decline. The importance of the mid-1970s for widespread downturns was emphasized by a further analysis of the population change data: more negative population changes occurred across species between 1976 and 1995 than between 1968 and 1975 (Siriwardena *et al.* 1998a). Compilation of a range of indicators of agricultural practices and land-use using multivariate analysis has shown that agricultural intensification in general was rapid between 1970 and 1988, and particularly so between 1975 and 1986 (Chamberlain *et al.* 1999, Fuller 2000).

RELATING TRENDS TO DEMOGRAPHIC RATES

The mechanisms by which environmental change has affected the abundance of farmland birds will have involved changes in one or more of four classes of demographic rate: survival, productivity, immigration and emigration. Farmland makes up most of the landscape in Britain, so comparatively small fractions of the populations of the bird species that are typical of farmland are generally found in other habitats (Gregory & Baillie 1998). Together with estimates of dispersal distances from bird ringing data (Paradis *et al.* 1998), this suggests that the net effects of immigration and emigration can safely be neglected in analyses at the national scale. Long-term historical BTO data on survival (from ring-recoveries) and on fledgling production per nesting attempt (from nest records) then allowed us to investigate temporal changes in these key demographic rates with respect to the trends in abundance

revealed by the CBC. Information on two components of the overall annual productivity of fledged independent offspring, the number of breeding attempts made and the post-fledging survival rate, was not available directly.

Analyses of survival rates

To investigate survival rates, we analysed the BTO's databases of ring-recoveries from dead birds (i.e. excluding recaptures and sightings of marked birds). Although much ringing activity has not taken place on farmland *per se*, limiting the extent to which the ringed sample can be considered representative of "farmland" populations, the ubiquity of farmland in Britain means that a large proportion of individuals will encounter it (and be affected by farmland management), at least during winter or during dispersal or migration. We found that recovery sample sizes were large enough to support analyses of annual variations in survival rate for only six seed-eating species: Bullfinch, Chaffinch, Goldfinch, Greenfinch, Linnet and House Sparrow (Siriwardena *et al.* 1999). This list nevertheless encompassed a range of long-term population trajectories (see Introduction). To estimate survival rates, we fitted models to ring-recovery data that allowed annual and age-specific (adult/first year) variation in survival rates (after Lack 1951, Haldane 1955, Aebischer 1987) from 1962 onwards. Such models contain an implicit assumption that the reporting rate, i.e. the probability that a dead ringed bird will be found and reported to the BTO, has not changed over time within cohorts. We were able to test this assumption by investigating the variations in annual reporting rates between 1985 and 1994 (using age-specific ringing totals data: Baillie & Green 1987, Baillie & McCulloch 1993) for four species: Bullfinch, Chaffinch, Greenfinch and Linnet. We found no significant annual time-dependence in reporting rate for any of these species (although the software available at the time did not permit explicit testing for temporal trends) and significant age-dependence occurred only in the data for Greenfinch (Siriwardena *et al.* 1999). We checked whether the latter effect had important implications for our subsequent analyses and found that it did not: correcting for it did not alter the implications of the results (see below).

Our recoveries-only models using data from 1962 onwards (and not estimating reporting rates) showed that significant annual variations in survival rates had occurred for all species except Linnet and that there was significant dependence on age-class for all species except Linnet and Goldfinch (Siriwardena *et al.* 1999). To reveal the implications of the variations in survival rates for changes in abundance, we entered the annual estimates of adult and first-year survival rates for each species into simple population models (which assumed constant productivity over time). We then compared the resulting "predicted"

population trends with the CBC indices to reveal whether the changes in survival rates could have driven the major changes in abundance. To do this, the constant estimate of productivity (per individual) for each species was varied iteratively to obtain the closest possible fit between the CBC and model index series (whilst ensuring that the estimates of productivity remained realistic).

The population trends indicated by the CBC and our models were very different for Bullfinch, Chaffinch, Greenfinch and Linnet, implying that the variations in survival rates revealed by our models (subject to the models' limitations) could not explain the major variations in abundance on farmland that have occurred. However, much better fits were apparent in the data for Goldfinch and House Sparrow (Fig. 2), suggesting that variations in survival rate *do* underlie the changes in the populations of these species. (Note that we were only able to compare data from 1976 onwards for House Sparrow because CBC data were not collected earlier; the available evidence suggests, however, that the population was more stable before the mid-1970s: Summers-Smith 1988, Glue 1994). We could also improve the fit of the Goldfinch model

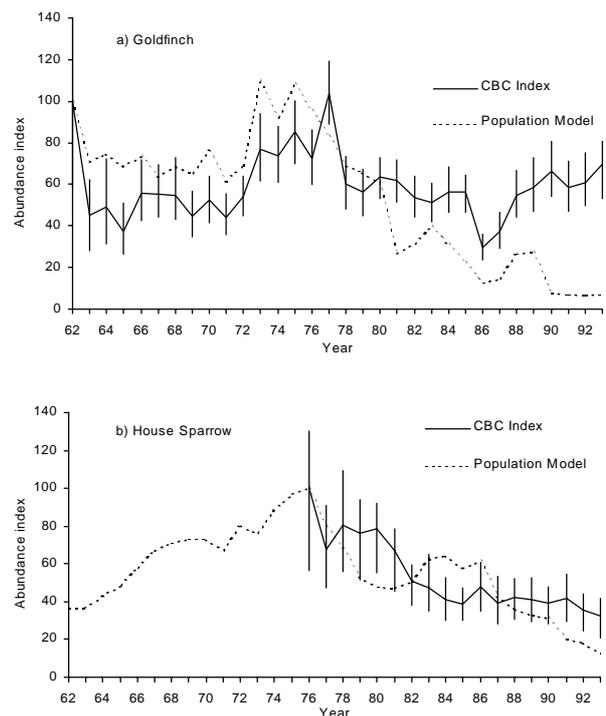


Figure 2. Unsmoothed farmland CBC trends and population models (1962-1995) for (a) Goldfinch and (b) House Sparrow. Population models were constructed from annual estimates of adult and first-year annual survival rates and a constant estimate of the annual productivity of fledged, independent juveniles, given a starting index value of 100. Initial estimates of productivity were estimated from periods of stability in the CBC trends and their associated survival rates; these values were then varied iteratively to produce the closest fit between the CBC and model trends for each species. See Siriwardena *et al.* (1999), from where this figure is adapted, for details of the method.

where it diverges from the CBC trend in the last ten years of the time series simply by increasing productivity in that period by a very small amount (from 1.77 to 1.80 fledged young per individual per year). Similar results to ours for Goldfinch and House Sparrow were found for Song Thrush by Thomson *et al.* (1997). Such positive results, i.e. those that demonstrate close fits between the models and the CBC, provide stronger evidence than negative ones: any difference between the populations sampled by the CBC and the ringing scheme and any other sources of error will tend to cause a lack of fit rather than a spurious good fit.

We checked the modelling results using another form of survival analysis, in which we estimated survival rates with respect to CBC trend direction. We divided up smoothed long-term CBC trends (1962-1994) according to when significant turning points occurred in the time series (see above) and classified the periods between turning points according to trend direction: population growth rate positive, effectively zero or negative. The survival models we fitted allowed survival rates to vary only with respect to trend direction (so that one survival rate was estimated for periods of increase, one for stable periods and one for declines), allowing us to test explicitly whether there were significant associations with long-term population trend. If survival rates had been higher when population trends were more positive, it would suggest that changes in survival rates could have driven the population trends.

The results of these tests were mostly consistent with the results of the modelling analyses and are described in full in Siriwardena *et al.* (1999). Goldfinch and House Sparrow survival rates were lower during periods of decline for each species, while there were no significant differences with respect to trend direction for Bullfinch, Greenfinch and Linnet. The trend-specific model for Chaffinch revealed a marginally significant reduction in adult survival rate during the recent period of stability in the CBC trend (from 1988 onwards), suggesting that the reduction could have contributed to the cessation of the species' increase (Siriwardena *et al.* 1999).

Such year-block or trend-specific models can be fitted to smaller ring-recovery data sets than are required for models estimating survival rates annually. We took advantage of this to investigate the importance of survival rates in determining population trends for a wider range of farmland birds (Siriwardena *et al.* 1998b). We considered as many species found on farmland as we could (a total of 28), including some species (e.g. Blackbird *Turdus merula*) for which sample sizes would support much more detailed analyses (Table 4). We could then look for interspecific patterns in the role of variation in survival rates in farmland bird demography.

Survival rates tended to vary with age, with adult survival rates being higher than those of first-years (a

significant difference across species), as might be expected (Table 4, Siriwardena *et al.* 1998b). There was also significant variation in survival rates with respect to trend direction for 16 of the 28 species tested and, for 13 of these, the variation was consistent with it having contributed to the farmland population trends of the species concerned (Table 4). These species were Pied Wagtail *Motacilla alba yarellii*, Robin *Erithacus rubecula*, Blackbird, Song Thrush, Mistle Thrush *Turdus viscivorus*, Lesser Whitethroat *Sylvia curruca*, Whitethroat *Sylvia communis*, Blue Tit *Parus caeruleus*, Great Tit *P. major*, House Sparrow, Chaffinch, Goldfinch and Redpoll *Carduelis flammea*. In itself, this result suggests that changes in annual survival rates have been important in determining population trends in farmland birds, but it may also underestimate this importance. The analyses for several species will have been low in power because the available ring-recovery sample sizes were small, and the inclusion of off-farmland birds in the ringed sample could have obscured relationships between survival rate and the CBC trend in some cases. Survival might therefore have been important for further species, such as Reed Bunting and Yellowhammer. Analyses of long-term mark-recapture data for Reed Bunting have shown that variations in annual survival rate can explain that species' population trend (Peach *et al.* 1999). Our estimates of trend-specific Yellowhammer survival rates, although not significantly different from one another, suggest a fall in survival rate during the species' decline that has been found to be sufficient to explain the decline, given estimates of breeding success (which has been high in recent years, at least) from intensive field studies (Kyrkos 1997, Bradbury *et al.* in press).

Analyses of fledgling production per nesting attempt

We analysed data from the BTO's Nest Record Scheme for twelve seed-eating species, Stock Dove, Turtle Dove, Tree Sparrow, Skylark, Linnet, Chaffinch, Goldfinch, Greenfinch, Bullfinch, Reed Bunting, Yellowhammer and Corn Bunting, using nest record habitat data to restrict the sample to cards from farmland. Variations in fledgling production per nesting attempt (hereafter, "fledgling production") were investigated with respect to CBC trend direction using methods similar to those applied in our analyses of survival rates. We measured fledgling production in terms of clutch size, brood size, chick:egg ratio (the ratio of maximum brood size recorded to maximum clutch size recorded) and daily nest failure rates during the egg period and the nestling period. Since contrary variations in these parameters could cancel each other out, we also calculated the number of fledglings produced per breeding attempt as a composite of the

variables we had measured directly. The data were often too sparse to allow annual estimates of fledgling production parameters to be made reliably, so we again used periods of consistent CBC trend direction, as delimited by the significant turning points we had identified, to investigate temporal variation. (Note that parameters were estimated for individual periods, not for combinations of all periods with the same trend direction.) We used nest record data from 1962 to 1995 to match the period covered by the CBC. The nest record data set provides good coverage of lowland Britain with little geographical bias, but it tends to undersample late-season nests (although

there is no evidence that the extent of this undersampling has varied over time). Crick & Baillie (1996) provide a comprehensive review of Nest Record Scheme methodology.

Various significant differences in components of fledgling production were found with respect to trend period and these translated into large differences in numbers of fledglings per attempt for most species (Siriwardena *et al.* 2000a). However, we found clear differences consistent with the hypothesis that variation in fledglings per attempt had driven population trends for only one species: Linnet (Fig. 3a). This pattern was

Table 4. Age-specific survival rate estimates for each species for periods of increasing, stable and declining CBC trend. Significance tests were made by comparing models with both likelihood-ratio tests and Akaike's Information Criterion: "Both" indicates where both approaches gave a significant result, "LRT" where only the likelihood-ratio test showed a difference, "AIC" where only Akaike's Information Criterion suggested a difference, ns where neither did. LRTs and AIC provide complementary perspectives on model selection: the former allow tests of specific hypotheses, while the latter considers parsimony (the number of parameters used) as well as model fit. For species shown in bold, significant variations in survival rates were consistent with their having had a role in driving population trends. Adapted from Siriwardena *et al.* (1998b), with the addition of data on Turtle Dove.

Species	Annual survival rates						Significance of variation with	
	Adult			First-year			Age	Time
	Increasing	Stable	Declining	Increasing	Stable	Declining		
Turtle Dove	-	0.623	0.525	-	0.222	0.185	Both	ns
Swallow	0.379	-	0.367	0.388	-	0.408	ns	ns
Pied Wagtail	0.499	0.477	-	0.442	0.352	-	Both	Both
Wren	0.313	0.314	0.329	0.314	0.230	0.256	LRT	ns
Dunnock	0.468	0.486	0.466	0.369	0.322	0.355	Both	ns
Robin	0.427	0.421	0.396	0.435	0.396	0.396	ns	AIC
Blackbird	0.686	0.667	0.630	0.562	0.601	0.537	Both	Both
Song Thrush	0.655	0.572	0.530	0.528	0.498	0.371	Both	Both
Mistle Thrush	0.813	0.635	0.586	0.417	0.618	0.573	Both	Both
Sedge Warbler	-	0.284	0.205	-	0.233	0.257	ns	ns
Lesser Whitethroat	-	0.728	0.317	-	0.615	0.354	ns	Both
Whitethroat	0.424	0.439	0.197	0.306	0.301	0.192	Both	Both
Blackcap	0.440	0.411	-	0.364	0.271	-	Both	ns
Chiffchaff	0.189	0.375	0.335	0.182	0.344	0.201	AIC	AIC
Willow Warbler	0.326	0.271	0.339	0.240	0.225	0.252	Both	ns
Long-tailed Tit	0.490	0.413	0.368	0.261	0.212	0.300	Both	ns
Blue Tit	0.574	0.513	-	0.411	0.365	-	Both	Both
Great Tit	0.560	0.572	0.460	0.395	0.419	0.312	Both	Both
Starling	-	0.690	0.806	-	0.522	0.614	Both	Both
Tree Sparrow	-	0.376	0.269	-	0.451	0.526	Both	ns
House Sparrow	-	0.582	0.500	-	0.526	0.333	Both	Both
Chaffinch	0.597	0.532	-	0.528	0.525	-	Both	Both
Greenfinch	0.414	0.471	0.449	0.409	0.441	0.403	ns	Both
Goldfinch	0.440	-	0.345	0.370	-	0.327	ns	Both
Linnet	0.360	-	0.383	0.320	-	0.367	ns	ns
Redpoll	0.437	-	0.334	0.474	-	0.386	ns	Both
Bullfinch	0.437	0.387	0.414	0.327	0.321	0.356	Both	ns
Yellowhammer	0.557	0.535	0.449	0.522	0.556	0.440	ns	ns
Reed Bunting	0.542	0.542	0.538	0.558	0.427	0.469	Both	ns

caused by an increase in the daily nest failure rate in the egg period during the major period of decline (1975-1986) (Siriwardena *et al.* 2000a) that was large enough to have driven the decline (S.N. Freeman & H.Q.P. Crick unpubl.). A much more common pattern was for number of fledglings per attempt to be *higher* during population declines (Fig. 3b-f), suggesting that changes in fledgling production were not their causes. The results for the other species investigated were less clear, showing changes in fledgling production which, at most, may have contributed to changes in trend direction but could not have driven long-term declines or increases (Siriwardena *et al.* 2000a). The clearest such pattern suggested that increased egg period failure rates contributed to the stabilisation of Chaffinch abundance after 1988 (thus adding to the effect of falling survival rates identified above).

Numbers of breeding attempts and post-fledging survival

All of our fledgling production results refer only to the productivity of fledglings *per breeding attempt*. Annual productivity clearly depends on the outcome of more than one breeding attempt per pair for many species (and all of the species considered can at least sometimes be multi-brooded: Cramp 1985, 1988, Cramp & Perrins 1994a,b). No direct measure of the number of breeding attempts made was available from nest records. In addition, our ring-recovery analyses for first-year birds made use only of individuals ringed as fledged independent juveniles: the average post-fledging age of birds ringed as juveniles can be as great as two months (Thomson *et al.* 1999). Survival rates over this post-fledging period therefore contribute to “productivity” as defined in the population models we applied to estimated survival rates, and are not measured by nest records.

We attempted to investigate the possible importance of these two unknown components of productivity using population models derived from those used to display the implications of variations in survival rates (Siriwardena *et al.* 2000a). Knowing changes in abundance (from the CBC) and variations in annual survival rates, we were able to estimate the annual productivity necessary to produce the observed long-term CBC trends for nine species. We then compared these predicted productivities with the fledglings per attempt figures derived from nest records: the differences reflected the likely combined importance of factors influencing annual productivity that were not incorporated in the estimates of per attempt fledgling production from nest record data. The number of breeding attempts made and the post-fledging survival rate are two of these factors, but others potentially include changes in the proportion of adults breeding, changes in the population sex ratio and any sources of error or bias in

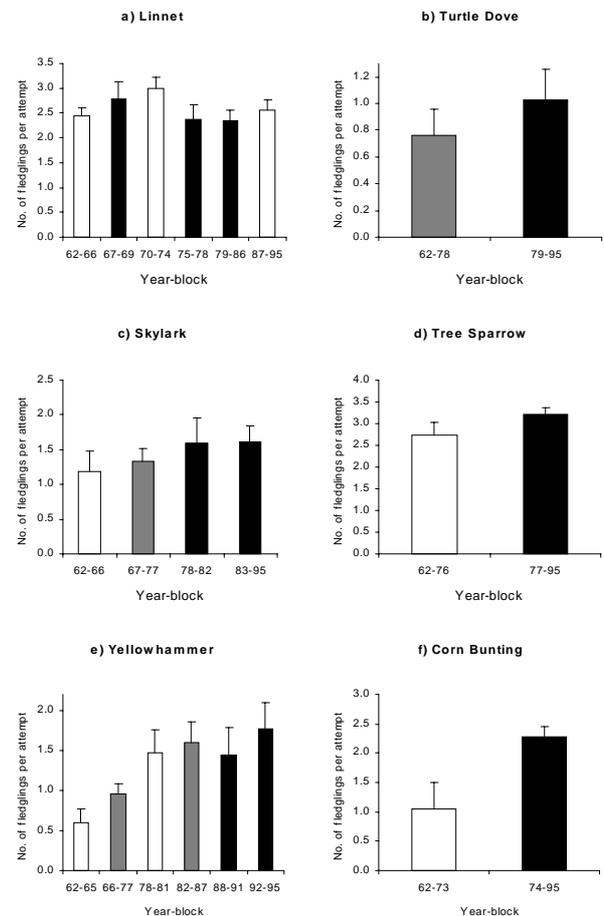


Figure 3. Graphs summarizing temporal variation in fledgling production for six species. Each bar shows the number of fledglings produced per nesting attempt in a period of consistent trend direction identified from the species' smoothed CBC trend. White bars denote periods of increase, striped bars periods of stability and black bars periods of decline. Error bars show 95% confidence intervals. Linnet (a) was the only species for which variation in breeding performance appeared to have driven population changes; for Turtle Dove (b), Skylark (c), Tree Sparrow (d), Yellowhammer (e) and Corn Bunting (f) fledgling production was higher during population declines. The results for Bullfinch, Chaffinch, Goldfinch, Greenfinch, Reed Bunting and Stock Dove showed no clear associations with trend direction. Adapted from Siriwardena *et al.* (2000a).

the data. We could not separate these variables or estimate their importance individually, but the results showed that variation in some of these unknown factors was required to explain trends in abundance for seven species: Bullfinch, Chaffinch, Goldfinch, Greenfinch, Linnet, Reed Bunting and Yellowhammer (Siriwardena *et al.* 2000a). One or more of the unknown parameters could therefore have played a central role in mediating population change for the species (such as Greenfinch) for which we have not identified other demographic mechanisms, and could have contributed to relatively minor population changes for the other species (such as the brief period of decline in Linnet abundance between 1967 and 1969). Only for Turtle Dove and Tree Sparrow did it appear that almost all the observed underlying long-term CBC trend could be explained by variations in annual survival rate and fledglings per attempt alone (Siriwardena *et al.* 2000a).

DEMOGRAPHIC RATES AND AGRICULTURAL LAND-USE

Given the apparent importance of annual survival rates in the demography of population change in farmland birds, it would have been useful to investigate the influences of land-use on mortality. However, spatial information in the BTO ring-recovery data set is limited to ringing and finding locations that cannot reliably be linked to habitat data from the areas in which birds have spent most of their lives. We were able to investigate the effects of agricultural land-use on fledgling production, and we conducted two sets of analyses using nest record data with habitat information from three sources. First, the effects of the spatial scale and the overall farming regime were investigated using data available in nest records on the habitat immediately surrounding each nest (Baillie 1988, Crick *et al.* 1994) and data on landscape composition (arable or pastoral) from the Institute of Terrestrial Ecology (ITE) Landscape Region classification (derived from ITE Land Classes) at the scale of 10-km squares (British National Grid) (Barr *et al.* 1993). Second, the effects of the detail of agricultural land-use at the scale of 10-km squares were investigated using data from the June Agricultural Census conducted by the UK Ministry of Agriculture, Fisheries and Food (for England and Wales) and the Scottish Office Agriculture and Fisheries Department (for Scotland). As with our earlier analyses of nest records, we investigated the variation in five components of fledgling production (clutch size, brood size, chick:egg ratio, egg period daily nest failure rate and nestling period daily nest failure rate) and (where possible) in the composite measure of numbers of fledglings produced per attempt. Although our earlier analyses had suggested that changes in fledgling production have not been a key factor underlying most major granivorous farmland bird population trends, any relationships found could still have influenced more minor changes in abundance. They could also point to areas where useful remedial conservation action might be applied and show how relationships with particular land-use patterns are reflected at the national scale.

Scale, farming regime and time

We used nest record habitat data and ITE Landscape Regions to investigate the effects of farming regime on fledgling production at the territory (habitat immediately surrounding the nest site) and landscape scales, respectively, and to investigate the variation (at the territory scale) between early (1962-1975) and late (1976-1995) years in the period covered by the CBC (Siriwardena *et al.* 2000b). We examined fledgling production data (including numbers of fledglings per attempt) for ten

species: Stock Dove, Skylark, Tree Sparrow, Chaffinch, Greenfinch, Linnet, Bullfinch, Reed Bunting, Yellowhammer and Corn Bunting (sample sizes for Goldfinch and Turtle Dove were prohibitively small). The landscape-scale analyses compared fledgling production between arable and pastoral 10-km squares, using data from 1990 onwards (the period for which grid references were readily available in nest record data). The analyses at the territory scale compared arable, grazing and mixed farmland using data from 1962 onwards.

In general, associations between farmland type and both fledgling production and changes in fledgling production over time were species-specific, suggesting that farmland habitat tends to influence each species differently (Siriwardena *et al.* 2000b). However, there were a few patterns that were common to small numbers of species. For example, improvements over time in fledgling production at the territory scale occurred across all three farming regimes for four declining species (Skylark, Bullfinch, Yellowhammer and Corn Bunting). Reductions in Linnet fledgling production at the territory scale were found on grazing land (but not on arable or mixed farmland), and reductions in Reed Bunting fledgling production occurred on arable/mixed farmland only (arable and mixed farmland had to be combined for Reed Bunting to provide an adequate sample size).

Different relationships between farming regime and fledgling production were found at the two spatial scales. This was not unexpected because the heterogeneity of the British lowland landscape is not the same at different scales: a description of the habitat in any given patch of 50-100 m² (the likely size of the habitat recording area for nest records) is unlikely also adequately to describe the habitat across the 10-km square in which it falls. Pastoral landscapes were associated with significantly higher overall fledgling production for Corn Bunting, Linnet and Skylark, and with higher values of one or more individual components of fledgling production for Reed Bunting, Stock Dove and Tree Sparrow. Five of these six species have undergone large declines. Arable landscapes were associated with higher fledgling production only for Chaffinch and Greenfinch, species whose populations have been stable or increasing. Mixed farming was associated with higher fledgling production for four species, three of which (Bullfinch, Yellowhammer and Corn Bunting) have declined concurrently with the frequency of mixed farms.

Detailed agricultural land-use

Using newly-computerized information on Nest Record Card (NRC) geographical locations for six granivorous species that have undergone large declines (Skylark, Tree Sparrow, Linnet, Bullfinch, Reed Bunting and Yellowhammer), we combined Agricultural Census data on crops and land-use with fledgling production data from

1967 to 1994: agricultural data from one of eight census years were assigned to each NRC by year (using the census year closest in time to that in which the NRC was completed) and 10-km square grid reference (Siriwardena *et al.* in press). We then related the five components of fledgling production to land-use. We used a principal components (PC) analysis to describe the overall variation in agricultural land-use as parsimoniously as possible and found that five PC axes were sufficient to describe 67% of the spatial and temporal variation from 1969 to 1988. We then tested the importance of these PC axes, i.e. of land-use in general, for fledgling production using stepwise, multivariate, generalised linear models. We also conducted univariate analyses with respect to crop diversity, landscape heterogeneity (the mix of arable and grazing land), the proportion of farmland that was arable, the area of fallow land, the proportion of barley sown in spring and the area of rape (Linnet and Reed Bunting only) to test hypotheses about the effects of specific land-uses or practices.

The five different PC axes explained the variation in fledgling production to varying degrees across species, some different association with agriculture being found for each species (Siriwardena *et al.* in press). Within these species-specific combinations of PC axes, one notable generality was for positive associations with a PC axis describing a gradient from re-seeded to established pasture and from less to more of an arable component in the landscape. This result suggests that reductions in land-uses characteristic of mixed and less intensive pastoral farmland have had negative effects on fledgling production for Linnet, Bullfinch, Reed Bunting, Skylark and Yellowhammer. Other PC axes were associated with fewer species and in more diverse ways, suggesting interactions between habitat and species ecology (Siriwardena *et al.* in press). In general, these results could provide hypotheses for intensive studies and frameworks for predictive modelling of the impact of agricultural land-use on avian breeding success.

The individual agricultural variables tested also produced diverse results across species, but with some notable common patterns (Siriwardena *et al.* in press). High crop diversity and/or high landscape heterogeneity were associated with higher fledgling production via one or more parameters for all species except Reed Bunting, as were larger areas of fallow land for Tree Sparrow, Linnet and Reed Bunting. Rape crops were associated with negative effects on Linnet fledgling production (through the daily nest failure rate in the egg period). There were no clear, interspecific patterns in the results for the proportion of farmland under arable land-use or for the proportion of barley that is sown in spring, and it was common even within species for these variables to have conflicting influences on overall fledgling production through different nest record parameters.

DISCUSSION

Population trends

Our failure to find large clear groups of species with similar trends suggests that changes in the environment (interacting with internal population processes such as patterns of density-dependence) have affected species differently according to their ecological specialisations. Our results therefore suggest that large numbers of farmland bird declines or increases cannot be attributed to single simple agricultural or environmental causes and mechanisms. However, the differences in population processes and ecology mentioned above also mean that somewhat different trends for two or more species could result from similar environmental impacts on the same demographic rate. The number of species found to have population trend patterns in common with several others (Table 3) may therefore underestimate the true degree of interspecific generality in demographic causes and mechanisms, but these groups would then be particularly unlikely to have arisen by chance. The evidence for common changes in trend direction (and therefore also perhaps in demography), which is apparent when changes are examined on a year-by-year basis (Fig. 1), supports the idea that environmental effects could have been rather more general during certain periods than our long-term analyses had suggested.

Survival

Our results suggest that changing survival rates represent, in general, the most important of the demographic factors investigated in driving farmland bird population change, and we may have underestimated their importance where sample sizes were small (Siriwardena *et al.* 1998b). Environmental changes that affect abundance through survival rates are therefore implicated as probably being more important across species than those that might act through fledgling production. Some independent evidence exists for the importance of survival in this context, although much of it is circumstantial: the evidence is summarised in Table 5.

For non-hunted species, survival rates are most likely to reflect changes in food availability, although actual causes of death may be related to the costs of feeding on suboptimal foods or of foraging in poor habitats for longer, rather than being direct starvation. The effects of key environmental changes may therefore be seen most clearly at times of the year when food stresses are most acute and natural “bottlenecks” for survival occur. The most serious bottlenecks may occur in periods of cold weather, when metabolic needs are high while daylengths, and therefore foraging opportunities, are at a minimum. For ground-

Table 5. Evidence from other studies as to the importance of changes in survival rates and fledgling production in determining farmland bird population trends. Scientific names not given here can be found in Table 2.

Species	Evidence
Effects of Survival	
Loggerhead Shrike <i>Lanius ludovicianus</i> *	Population modelling suggests that a steep decline is best explained by a reduction in survival rates (Brooks & Temple 1990).
Cirl Bunting	Increase after habitat provision suggests that abundance in Britain has been limited by winter survival, owing to food availability (Evans 1997).
Stock Dove	Increase consistent with hypothesis of a decreasing impact of poisoning from organochlorine seed-dressings on adult survival (O'Connor & Mead 1984).
Swallow, Sedge Warbler, Whitethroat, Blackcap, Willow Warbler, Redstart <i>Phoenicurus phoenicurus</i> , Pied Flycatcher <i>Ficedula hypoleuca</i> †	Inter-annual changes in the CBC abundance of these seven Palaearctic-African migrants mostly due to differential losses of fully grown birds (shown by key-factor analysis: Baillie & Peach 1992). Consistent results for Sedge Warbler and Willow Warbler from mark-recapture data (Peach <i>et al.</i> 1991, 1995).
Effects of Fledgling production	
Kestrel <i>Falco tinnunculus</i> , Blackbird, Song Thrush, Starling, Willow Warbler, Dunnock, Treecreeper	Increases in productivity during (at least slight) farmland population declines shown by nest records and/or constant effort ringing (Baillie 1990, Crick <i>et al.</i> 1998) suggest that productivity has not driven the changes.
Blackcap, Chiffchaff, Magpie, Jackdaw, Carrion Crow	Recent population increases have been accompanied by increases in fledgling production (from nest records: Crick <i>et al.</i> 1998).
Lapwing, Snipe <i>Gallinago gallinago</i> , Black-tailed Godwit <i>Limosa limosa</i> , Redshank <i>Tringa totanus</i> , Ruff <i>Philomachus pugnax</i>	For all five species in the Netherlands and for Lapwing in northern England, productivity is lower under recent, intensive, agricultural regimes (Beintema 1988, Baines 1989, Beintema <i>et al.</i> 1997). Declines of Lapwing and Snipe in Britain were associated with falling fledgling production (Shrubb 1990, Crick <i>et al.</i> 1998), while Lapwing survival rates increased (Peach <i>et al.</i> 1994). Low Lapwing productivity is due to increased nest losses from trampling and from predation caused by diminished cooperative defence (because low invertebrate densities lead to low breeding densities; Shrubb 1990, Berg <i>et al.</i> 1992). Declines in spring sowing and mixed farming may also have been critical: productivity is poorer in autumn-sown crops and adjacent pasture provides chick-feeding habitat (Beintema 1988, Galbraith 1988, Beintema <i>et al.</i> 1997).
Stone-curlew <i>Burhinus oediconemus</i>	Low productivity due to direct mortality of chicks from agricultural operations has contributed to the decline (Green & Griffiths 1994).
Corncrake <i>Crex crex</i>	Low productivity due to direct mortality of chicks from agricultural operations is a major cause of decline (Stowe <i>et al.</i> 1993, Green <i>et al.</i> 1997).
Grey Partridge	Low productivity through reductions in the availability of invertebrate food resulting from herbicide applications on the weeds on which the invertebrates feed is a major cause of decline (Potts 1986).
Sparrowhawk <i>Accipiter nisus</i>	Low and then recovering productivity (driven by the effects of bioaccumulated organochlorines on eggshell thickness) caused recent population trends for this and other British raptors (Newton 1979).

* A species found in North American lowland farmland.

† The first five of these species occur commonly on lowland farmland and were considered in our analyses, but only for Whitethroat did we identify analogous relationships between survival and *long-term* trends in abundance. This disparity shows that relationships between demography and population changes can be complex and can depend on the timescale investigated.

foraging species, frosts can also restrict feeding opportunities severely. Clearly, all these factors will be most significant in winters when the weather is especially harsh. Late winter or early spring can also be a critical period, especially for granivorous species, because stocks of food remaining after the previous summer will have been depleted to their lowest levels just when costly pre-breeding activities such as territory acquisition and competition for mates are of paramount importance.

Factors directly affecting food availability in bottleneck periods may therefore provide strong initial hypotheses as to the causes of many species' declines. We were unable to investigate how these critical causes of mortality interact with relationships between survival rates and land-use, and we could find no other studies in the literature where such analyses had been conducted. In addition, it is possible that the causes of decline have not acted in the bottleneck periods themselves: environmental impacts such as habitat deterioration in the breeding season (say, increasing the costs of chick-feeding or nest defence or delaying the start of breeding so as to reduce later fat deposition) could potentially compromise birds' abilities to withstand winter conditions. The low annual survival rates of many small farmland passerines (often below 50%; Siriwardena *et al.* 1998b) mean that natural selection might favour individuals who invest in productivity ahead of overwinter survival.

Fledgling production per nesting attempt

Responses to environmental stresses in the breeding season of the kind discussed above could partly explain why we found few signs of declines in fledgling production in granivorous farmland bird populations. Other analyses of nest record data suggest that a similar pattern applies to a wider range of nidicolous farmland bird species (Table 5). These widespread patterns for increased fledgling production in declining species clearly suggest that changes in the various components of this demographic rate cannot be implicated as a general mechanism underlying the species' declines. However, they also raise a question as to what has caused the increased performance that is evident in nest record data. There are several possible explanations for this pattern, including density-dependent effects, and these are discussed in detail in Siriwardena *et al.* (2000a). It is notable that studies of declining nidifugous farmland birds have tended to reveal a different pattern, strong correlations between population changes and measures of productivity being common (Table 5). Similar correlations are also apparent in changes in productivity for increasing nidicolous species (Table 5).

Among the nidicolous seed-eaters that we investigated, the Linnet's decline was the only population change explicable by a reduction in numbers of fledglings per

attempt, which was caused by higher daily nest failure rates during the egg period. This effect was large enough, alone, to have caused the observed decline (S.N. Freeman & H.Q.P. Crick unpubl.). Our analyses of the influences of agriculture on fledgling production revealed two variables that had significant effects that (if real) will have led to increases over time in the egg period daily nest failure rate: the area of oilseed rape (the stronger effect) and a principal component axis dominated by rape and livestock numbers (Siriwardena *et al.* in press). This suggests that increases in the areas of rape in 10-km squares have been associated with the Linnet's decline. We have also found that a crude measure of Linnet abundance in 10-km squares (based on breeding bird atlas data: Gibbons *et al.* 1993) is also negatively related to the area of rape (Siriwardena *et al.* in press). This pattern is surprising because rape seed is currently important in the diet of nestling Linnets (Moorcroft *et al.* 1997, Eybert & Constant 1998) and could have allowed some recovery in the species' population (Moorcroft & Wilson 2000). In fact, this apparent contradiction may reflect differences between good and poor Linnet habitat. Good habitat may be characterized by the availability of hedgerow nest sites and weed seed foods associated with the grassland component of mixed farmland (e.g. dandelions *Taraxacum* spp.); such an environment might still be enhanced by a rape seed food source. Areas where rape is most common may generally be poor Linnet habitat, the availability of rape being insufficient to mitigate adverse features of the environment such as intensive wheat cultivation. The increase in the annual average egg period failure rate in such poor habitats could reflect higher desertion or predation rates, or a curtailment of the breeding season that prevents the successful completion of more productive late-season nests (Moorcroft & Wilson 2000).

Despite the general pattern, in our results and elsewhere, for the fledgling production of nidicolous farmland birds not to have been low during population declines, we found a range of relationships with agricultural practice suggesting that intensification has had a negative impact through this demographic rate. For example, we found evidence that mixed farming tended to have positive effects on fledgling production, as did landscape heterogeneity, crop diversity and areas of fallow land; all these features of less intensive agriculture have declined over time (Siriwardena *et al.* 2000b, in press). Consistent patterns, whereby fledgling production was found to be negatively affected by agricultural practices that characterise more intensive management, have also been found in other studies on a range of nidicolous species: Skylark (Schlöpfer 1988, Wilson *et al.* 1997), Starling (Tiainen *et al.* 1989), Cirl Bunting (Evans 1997, Evans *et al.* 1997), Lesser Kestrel *Falco naumanni* (Donazar *et al.* 1997), shrikes *Lanius* spp. (Lefranc 1997) and Corn

Bunting (Brickle & Harper 2000).

There is therefore an apparent anomaly between the changes that have occurred in fledgling production at the population level and the influences of agricultural changes on it. We suggest that this pattern has two non-exclusive explanations. First, although changing survival rates seem to provide an explanation for many long-term trends in abundance, changes in fledgling production could explain some of the variation around the trends that remains unexplained, even in our best survival models (Siriwardena *et al.* 1999). Second, although statistically significant, the effects of agricultural land-use on fledgling production may have been biologically insignificant in terms of driving population changes. Such a pattern would have important implications for studies that attempt to generalise up to the population level from local, intensive studies. Our results suggest that statistically significant associations between land-use and fledgling production can exist that are suggestive of mechanisms for population change, but that are unimportant at the population level. These results are particularly strong because we have found both sets of patterns in a single data set; the historical and population-wide context is unavailable to most intensive studies.

Unmeasured demographic rates

We were unable to measure post-fledging survival rates and the number of breeding attempts made by farmland seed-eaters, but we found some evidence that one or both had varied for seven of nine species tested. This evidence is only indirect and it is weak, being subject to several unverifiable (and perhaps unlikely) assumptions, and conceivably being entirely explicable by sampling errors in one or more of the demographic data sets (Siriwardena *et al.* 2000a). Nevertheless, it is clearly possible that variation in these demographic rates has had important effects on the productivity of independent young and thus on population trends. Several studies measuring productivity have found that the number of attempts made, rather than success per attempt, has had a greater influence (although individual quality is typically a confounding factor: see, e.g., Geupel & DeSante 1990, Møller 1990, Holmes *et al.* 1992). Few studies have investigated the importance of numbers of breeding attempts or of post-fledging survival, and still fewer have considered farmland birds. Preliminary evidence from ring-recovery analyses (using new methods: Thomson *et al.* 1999) and field studies suggests that falling post-fledging survival rates have contributed to the decline of the Song Thrush in Britain (D.L. Thomson pers. comm., W.J. Peach pers. comm.). Grassland-nesting waders have probably been seriously affected by changes in their habitat that restrict possibilities for laying replacement clutches

(Beintema 1988, Green 1988, Shrubbs 1990, Beintema *et al.* 1997). Reductions in the number of breeding attempts possible in the modern agricultural landscape may also have contributed significantly to the decline of the Skylark (Wilson *et al.* 1997). In addition, Skylark chicks leave the nest many days before they are able to fly (Cramp 1988), creating a significantly longer “post-fledging” period from the perspective of nest-based studies. Post-fledging survival rates might therefore be especially important for the Skylark and any other species with a similar breeding strategy.

Biases and other problems

The BTO data sets used have several characteristics that could have reduced the sensitivity of our analyses or introduced biases. Although we attempted to restrict our analyses as rigorously as possible to farmland habitats, some birds considered (especially in our survival analyses) will not have come from farmland. This will have weakened any relationships between the estimated demographic rates and population trends and thus made them more difficult to detect. Relationships will also have been less easily detectable where population changes have been small (e.g. for Greenfinch), because tests would probably have to detect small changes in the demographic rates responsible and such changes could easily be “lost” in sampling error. It is also possible, given density-dependence in a key demographic rate, that small ephemeral changes in the population-wide average could drive large changes in abundance (Green 1999, C.M. Perrins pers. comm.); such changes would again be difficult to detect. BTO data may be biased as a result of observer input into, for example, the selection of sampling sites for CBC counts or the timing of nest record selection. Clearly, no volunteer-based sampling system will be as good as a professional (and hypothetical) one based on a randomised sampling strategy, but criticisms of the imperfections in data collection should always be tempered by consideration of the strengths of the data sets, particularly with respect to the alternatives available (Table 1).

It is notable that all these problems and other sources of noise or sampling error in our analyses would tend to make results less significant and to obscure common patterns among species: any findings of generality are therefore likely to be more robust than those of specificity. Common patterns across sets of ecologically similar species also therefore lend weight to the results for each individual species in the set. This is important to note in cases where species-specific, short-term, local studies have produced results that could be regarded as contradictory to our findings (e.g. Brickle & Harper 2000).

Conclusions and future priorities

Our results, taken together with other information available on the demography of farmland birds, suggest that, if there is a general mechanism behind population changes (particularly declines) in nidicolous species, it lies in changes in survival rates. Nevertheless, nidifugous species may have been more affected by changes in fledgling production and some nidicolous species (such as Linnet) appear atypical. Despite these generalities, and even if particular environmental changes have had widespread common effects, interactions with species-specific ecological factors and population processes may then have made long-term trends more species-specific. As discussed above, however, we were unable to conduct strong tests of the importance of numbers of breeding attempts or post-fledging survival rates, reductions in either of which could have been critical for many species.

Our results suggest one clear direction for future farmland bird research: to investigate how agricultural land-use and management practices influence annual survival rates. The other clear need for future monitoring and intensive research lies in the investigation of post-fledging survival rates and the numbers of breeding attempts made in a season, with respect both to their importance in population demography in general and to their sensitivity to the effects of changes in the agricultural environment. Given the potential importance of density-dependent influences on changes in demographic rates (Green 1999), it would also be valuable to investigate how the agricultural environment affects such relationships with density (although studies of this kind would be difficult to conduct in practice). Further investigations of existing long-term BTO data sets can contribute to these research directions, but new data collection, ideally at the scale of whole farms, will also be necessary.

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