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# Status and population trends of Starling *Sturnus vulgaris* in Great Britain

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**Capsule** Starling populations have declined markedly since 1964, with the greatest declines in pastoral areas in the south and west of Britain.

**Aims** To establish the size of the Starling population and its recent decline in different habitats and regions.

**Methods** We use distance-based transect sampling to establish, for the first time, robust estimates of population size in different habitats and regions. We then analyse long-term trend data from two extensive monitoring schemes using generalized additive models to find correlates of the population decline.

**Results** The mean national breeding population of Starling over the period 1994–2000 was estimated at about 8.5 million birds, with a 95% confidence interval of 8.1–10.8 million. Most Starlings (36%) occur in southern Britain and densities are greatest in suburban habitats. Populations in both suburban areas and the wider countryside declined by over 50% between 1964 and 2000, being greatest in the south and west of Britain and in areas of livestock farming.

**Conclusions** Changes in pastoral farming practices are likely to account for at least some of the decline in the wider countryside, probably related to changes in food resources, though these are largely unquantified.

In Britain, and much of western Europe, the Starling Sturnus vulgaris is a familiar bird of both farmland and towns. However, there has been a decline in population numbers over the last twenty years, both in Britain and in the rest of Europe (Baillie et al. 2001, Hagemeijer & Blair 1997). Declines in other farmland birds are well known (Fuller et al. 1995), but most research has concentrated on the decline of arable specialists, in particular seed-eaters (Siriwardena et al. 2000, Robinson & Sutherland 2002). Although changes in arable farming have been large (Chamberlain et al. 2000, Robinson & Sutherland 2002), changes in pastoral farming have been just as great (Vickery et al. 2001). The Starling is very much associated with pastoral and livestock farming, where it has, in past times, been considered a pest species (Feare 1989), which could be controlled without a specific licence under a derogation of the Birds Directive (European Commission 1979).

Two populations of Starling occur in Britain (Feare 2002). The population that breeds in Britain is

resident, with birds largely remaining in the same general area throughout their adult life. During the winter months, this population is augmented by a similar number of immigrant birds that breed primarily in Sweden and the Baltic states (Lack 1986, Feare 2002). These birds arrive in October and November and depart in March. Here, we present an analysis of the changes in Starling abundance, using historical data from the British Trust for Ornithology's (BTO) Common Birds Census (CBC), together with more recent data from the BTO/Joint Nature Conservation Committee (JNCC)/ Royal Society for the Protection of Birds (RSPB) Breeding Bird Survey (BBS). The CBC monitored numbers of Starlings between 1964 and 2000 and has since been replaced by the BBS, which commenced in 1994 and has a wider and more representative geographical and habitat coverage.

We use these data sources to produce an estimate of the number of Starlings breeding in Britain, and to quantify the number and density of birds breeding in each region and habitat. We then examine the longterm population trends within different regions and habitats, with the aim of addressing a number of

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hypotheses. Do population trends differ between broad habitat types? Woodland habitat in particular is regarded as suboptimal since, although birds breed there, few forage there (Feare 1984). Have changes been greater in pastoral or arable systems? Foraging Starlings are often associated with livestock though rearing practices have changed markedly. Are declines greater on farms with livestock than without?

# **METHODS**

#### **Common Birds Census**

Until the inception of the BBS (see next section), the CBC was the mainstay of terrestrial bird monitoring in Britain (Marchant et al. 1990). From 1964 to 2000, between 200 and 300 plots were visited eight to 12 times each year and the positions of all birds were mapped by volunteer observers. These were converted by trained analysts at the BTO into the locations of breeding territories for each species. CBC plots were characterized as farmland, woodland or 'special' (the latter consisting of areas dominated by wetland, lakes, coastal habitat, etc.). On average, Starlings were recorded on 146 plots each year. Some more detailed habitat information was also recorded for each CBC plot, along with location and altitude data. Cropping patterns on farmland CBC plots have been shown to be representative of those across southern and eastern Britain (Fuller et al. 1985). We use both the complete CBC plot sample, and plots from farmland and woodland separately, to investigate long-term trends in breeding abundance.

### **Breeding Bird Survey**

The BBS was introduced in 1994 as a long-term replacement for the CBC. It was designed to improve on the CBC by providing wider, randomized spatial coverage that is representative of bird populations and habitats across the country. The BBS is based on  $1 \times 1$  km square survey units across which two 1-km transects are walked by volunteer observers twice between the beginning of April and the end of June each year; any birds seen or heard are recorded in distance bands (<25 m, 25–100 m and >100 m) on either side of the transects (Noble *et al.* 2001). Habitat is also recorded; the 2-km length of recording transect is divided into ten 200 m sections in each of which the habitat is characterized according to descriptions drawn from the standard BTO habitat coding system (Crick 1992).

# **Statistical methods**

The basic statistical framework employed is that of generalized linear and generalized additive modelling, each employing a log link function and a Poisson error distribution, as is appropriate for count data (ter Braak et al. 1994, Thomas 1996, Fewster et al. 2000).<sup>a</sup> Generalized linear models (GLMs) allow the modelling of annual variation and simple linear and quadratic trends, as well as analyses of the strength of relationships between abundance and various predictor variables, such as habitat characteristics. Generalized additive models (GAMs) allow the estimation of nonparametric smoothed trends, with a level of smoothing defined by the degrees of freedom, providing the best description of a long-term trend without imposing constraints on its shape (unlike linear, quadratic or other parametric functions; Fewster et al. 2000).

Smoothed CBC trends were produced for all plots, and for woodland and farmland plots separately. In addition, we produce plots for each of five regions of Britain and for arable-dominated, grass-dominated and mixed farmland CBC plots. The five regions were based on those used by Chamberlain *et al.* (1999) to compare intensive arable farming (in eastern England) with other agricultural types.<sup>b</sup> Other tests took the form, as appropriate, either of comparisons between linear year effect terms for different plot classifications or with respect to an additive (categorical) term.

BBS data were used to assess densities of Starlings with respect to habitat and region, using a distancesampling approach (Buckland et al. 1993, Thomas et al. 1998). This method incorporates modelling of how the probability of detection of a bird falls as distance from a transect line increases and allows these detection functions to be calculated on a habitat-specific basis (detectability is likely to vary between habitats due to differences in visibility and the efficiency of sound transmission). We calculated habitat-specific densities using the methods of Gregory & Baillie (1998). BBS data were assigned to broad habitat categories at the level of the 200 m transect section. Region- and habitat-specific subsets of the BBS count/distance-band data were then extracted and entered into the distancesampling analysis program DISTANCE (Thomas et al. 1998), taking the  $1 \times 1 \text{ km}^2$  sample square as the unit of analysis and considering the number of transect sections in the focal habitat in each square to reflect the length of transect sampled. In addition, we assumed that the random geographical coverage of the BBS (stratified by observer density; Gregory & Baillie 2004) allowed us to use BBS habitat records to estimate the area covered by each habitat category in each region and thus to produce estimates of regional and national population sizes by combining the area of each habitat in a region with region- and habitat-specific densities. Gregory & Baillie (1998) show that the BBS habitat data accord well with other measures of habitat area.

The greater amount of data available from BBS allowed a finer geographical split than was possible for the CBC analyses, so we were able to provide estimates for each of the ten British geographical regions used by the European Community for statistical purposes. Following Gregory & Baillie (1998), we estimated Starling densities from BBS data for each of 15 habitat categories: deciduous woodland, coniferous woodland, mixed woodland, scrub, semi-natural grassland, heath, improved grassland, unimproved grassland, mixed farming, arable farming, urban human sites, suburban human sites, rural human sites, areas adjacent to water bodies and miscellaneous areas. We conducted these analyses for each year for which BBS data were available, i.e. 1994-2000, calculating 95% confidence intervals for the region- and habitat-specific densities using a bootstrapping procedure in which survey squares were resampled, with replacement, 400 times (after Gregory & Baillie 1998). This enabled us to examine the variation in population trends among the regions and habitats occupied by Starlings to identify any population strongholds and problem areas for conservation.

### RESULTS

#### How many Starlings are there?

BBS data suggest that there are approximately 8.86 million starlings present in the breeding season (averaged over the period 1994–2000, 95% confidence limits: 8.14–10.82 million); however, these were not distributed evenly throughout the country (Table 1). Around one-third (36%) of all birds were recorded in the southernmost counties of England (south of a line from Essex to Gloucestershire), whereas Scotland (representing 33% of the land area) held only 21% of the population. These regional differences reflect, to some extent, differences in landscape character, the bulk of the population (73%) being found in areas dominated by gardens and unimproved grass.

The greatest densities of birds occurred in urban and suburban areas, with the density of birds in agricultural areas being an order of magnitude lower; densities in rural areas (i.e. villages) were intermediate (Table 2). There was no consistent geographical variation in the density in any habitat between regions, although the density of birds in Wales was low across all habitats and densities in suburban Scotland were particularly high.

In the wider countryside of Great Britain, i.e. away from human settlements, Starlings have declined by 68% since 1962 (Fig. 1; figures for population change are based on the GAM trends). The decline has been much greater in woodland CBC plots (92% since 1965) than farmland plots (66% since 1962), but because Starlings are more abundant on farmland plots, the

	Unimproved grass		Improved grass		Arable		Rural human		Suburban		Urban				A habi	 itats
	А	В	А	В	А	В	A	В	А	В	А	В	Wood	d Other	А	В
Scotland	4.33	+10.8	1.46	+14.1	1.80	-2.62	2.08	-1.09	5.36	-0.62	1.19	-2.75	0.36	4.32	20.90	+6.78
Northern England	1.08	-8.03	0.43	-12.0	0.41	-13.1	0.11	+0.93	1.71	-23.8	0.54	+26.4	0.17	0.42	4.87	-11.59
Northeast England	1.29	-9.53	0.64	+8.99	0.64	+2.42	1.64	-1.43	2.03	+12.9	0.72	-6.82	0.24	0.35	7.55	+1.51
Northwest England	1.48	-2.21	0.11	+2.18	0.53	-32.3	0.76	-4.97	2.13	+2.23	0.42	+7.27	0.01	0.51	5.95	+2.17
Wales	0.92	-41.8	0.03	+1.98	0.25	+20.8	0.47	+9.64	1.38	+18.8	0.31	+43.9	0.04	0.31	3.71	+5.04
Central west England	0.98	-16.6	0.48	-2.95	0.63	+9.48	0.71	+3.08	2.93	-8.58	0.85	-23.4	0.10	0.58	7.26	-4.50
Southwest England	2.57	+8.27	0.52	-11.9	0.67	-8.19	1.56	+1.87	2.71	-7.75	1.52	-8.71	0.05	1.05	10.47	-5.51
Central east England	0.89	+5.29	1.21	+0.29	0.24	-8.03	1.54	+2.62	3.15	+0.45	0.84	+0.95	0.06	1.46	9.21	+1.11
East Anglia	0.11	-6.80	1.02	-6.93	0.15	-1.94	0.09	-1.28	0.84	-2.19	1.10	+20.1	0.06	0.47	3.84	-3.23
Southeast England	2.10	-2.79	1.74	-8.62	0.89	-10.7	4.90	-0.52	11.17	-2.55	2.33	-2.31	0.41	2.31	25.85	-3.52
All regions	15.75	-6.53	7.64	+3.02	6.21	-0.53	13.86	-1.40	33.41	-1.20	9.82	-0.60	1.53	11.78	100	-0.85

Table 1. Population estimates by region and habitat for Starling as measured from BBS, during the period 1994-2000.

A, Percentage of the British population supported; B, mean annual percentage change. Changes in bold are significant at P < 0.05. Population change was not calculated for wood or 'other' habitats (a heterogeneous range of scrub, heath and coastal habitats) due to insufficient sample sizes.

	Unimproved grass	Improved grass	Arable	Rural human	Suburban	Urban
Scotland	36.9 ± 9.4	34.4 ± 3.2	14.2 ± 1.0	89.2 ± 13.9	291.4 ± 18.9	184.4 ± 19.1
Northern England	16.4 ± 1.6	20.6 ± 1.6	18.5 ± 3.5	140.7 ± 27.7	254.9 ± 33.6	140.1 ± 33.7
Northeast England	30.6 ± 3.6	46.3 ± 7.4	15.5 ± 2.1	110.4 ± 14.2	168.3 ± 13.5	242.8 ± 28.5
Northwest England	70.3 ± 11.6	55.9 ± 4.8	11.2 ± 2.3	89.4 ± 7.1	150.7 ± 5.0	128.4 ± 10.0
Wales	10.9 ± 2.9	9.3 ± 1.0	4.5 ± 1.1	41.8 ± 5.9	159.9 ± 8.7	108.4 ± 21.1
Central west Enaland	48.6 ± 9.4	24.1 ± 1.6	$14.8 \pm 1.3$	90.7 ± 2.2	206.5 ± 12.4	195.2 ± 8.0
Southwest England	$29.0 \pm 3.9$	27.9 ± 2.5	9.8 ± 1.4	96.5 ± 5.6	218.2 ± 10.0	$163.9 \pm 14.4$
Central east England	$30.9 \pm 5.8$	32.8 ± 4.7	$15.4 \pm 2.6$	102.5 ± 16.7	254.9 ± 13.6	245.9 ± 33.9
East Analia	44.6 ± 11.1	20.2 ± 2.9	$11.1 \pm 1.5$	105.8 ± 8.2	255.1 ± 18.9	104.1 ± 22.6
Southeast England	48.4 ± 5.2	47.5 ± 3.2	18.3 ± 1.91	$103.7 \pm 5.2$	245.0 ± 5.1	276.1 ± 3.2

Table 2. Density estimates by region and habitat for Starling as measured from BBS, for the years 1994–2000.

Density estimates in no./km $^2$  ± 1 se.

latter figure more closely resembles the overall trend. While the decline in woodland plots appears to have been largely continuous, a period of relative stability punctuated the decline in farmland populations in the 1970s. There were insufficient data to determine whether the early period of population increase on farmland plots (1962-65) occurred on woodland plots also. Population trends differed regionally, with declines being greatest in the southeast (Table 3). Although the average rates of decline in eastern and southwest England over the entire time period were lower than elsewhere, these declines started later (the starting points for the declines are 1986 and 1979 respectively), meaning that the rates of decline since then are greater than implied by fitting a simple linear trend.

Although there was an overall decline in number of birds recorded on all farmland CBC plots, this decline was not equal across farm types (Fig. 2). The decline was steepest on farms containing livestock (either alone, or in combination with arable crops), with declines on arable farms being less, though still significant (Table 3).

The timing of the declines has also differed between farm types. Numbers on mixed farms appear to have declined continuously since the mid-1960s, whereas numbers on grassland plots remained more or less stable until the late 1970s, only subsequently declining. Numbers in arable plots, however, show a large transient peak in the late 1970s and early 1980s. Although numbers have declined on these plots since 1980 (as elsewhere), numbers at the end of the time series show little difference from the early 1970s, particularly in the light of the wide confidence limits about the GAM trends. More generally, the declines tended to be steepest in the south of the country, and at lower altitudes (Table 3). There were no differences in trend between farmland plots with and without buildings.

As the BBS data only cover a short span of years, and sample sizes from some regions are small, regional habitat trends are apparently somewhat mixed (Table 1). Town populations seem to be generally doing best in the north and west of Britain, but are declining in the south. The significant decline in suburban areas in the southeast, the single most important region–habitat combination holding 11% of the total population, is suggestive of continuing problems for the British population in what may be its stronghold. Numbers on pastoral habitats in most regions are also generally declining, though again, populations seem to be faring better in the north.

# DISCUSSION

Here we present the first quantitative assessment of the number of Starlings breeding in Britain. Although often considered a bird of grasslands, about half of the British breeding population is found in towns and villages. The BBS recorded a population estimate of some 8.5 million birds breeding in Britain in the late 1990s. It is difficult (and of uncertain value) to convert the number of birds given here into number of pairs because Starlings are, to some extent, polygynous, and many birds do not breed in their first year (Feare 1984). Gates et al. (1993) estimated the number of Starling territories in Britain in 1990 at around 1.1 million, based largely on densities on 79 CBC plots. This is clearly an underestimate, since urban habitats, in particular, were poorly monitored. Assuming CBC plots monitor farmland and woodland only, they would census about one-third of the total population (Table 1). Accounting for this would give a population estimate of around 3.3 million territories. The BBS





**Figure 1.** Population index of Starling in Britain. Data from CBC for (a) all plots, (b) farmland plots and (c) woodland plots only. Solid line represents a smoothed GAM trend and the dashed line 95% confidence limits (see text for details). •, Annual indices (i.e. no smoothing);  $\bigcirc$ , significant (P < 0.05) turning points in the GAM trend.

counts all adult birds present in the square at the time of the survey and does not explicitly record the number of breeding territories as with CBC. In a species in which polygyny is common, each 'territory' will, on average, contain more than two adult birds. The 3.3 million territories derived from Gates *et al.* (1993) implies a total well in excess of 6.6 million birds, in line with the BBS estimate of 8.5 million birds which will also include any non-breeding birds present during the summer.

The decline of Starling populations has been greatest in woodland; CBC index for woodland plots has declined by over 90%. Starlings are obligate hole nesters, consequently woodland will be a prime nesting habitat. Although birds do forage in woodland, densities of soil invertebrates, their preferred prey, are likely to be lower and most woodland nesting Starlings probably forage on adjacent farmland (Feare 1984). Hence, woodland habitat probably represents a suboptimal habitat and the BBS indicates that densities in woodland average 7.9 birds per km<sup>2</sup>, much lower than in farmland or garden habitats. Thus, as the breeding population as a whole has declined, woodland habitat has been vacated preferentially. Consistent with this, the decline in woodland habitat appears to have preceded that in farmland habitats. However, changes in woodland structure such as less dead wood or greater ground cover resulting in fewer feeding areas, or perhaps increased nest predation, cannot be ruled out as contributory to the decline.

There is a clear decline in Starling numbers on livestock farms, whether these are entirely pasture based, or mixed with arable components (Table 3). Starlings frequently associate with livestock, particularly around stock-feeding areas, where they will feed on cereal grain (Feare 1984). Birds using these areas tend to remain faithful to a particular foraging site through the winter, whereas birds in arable areas tend to forage more widely (Feare 2002). Whilst the number of cattle has declined, sheep numbers have increased, which produces a different sward structure (Chamberlain et al. 2000, Fuller & Gough 1999). However, patterns of stock rearing are likely to have changed, with more raised indoors (particularly cattle), partly to reduce disease transmission by birds, and less use of fodder crops. This may have reduced the foraging opportunities available to Starlings, as supplementary foods will be less accessible. It is also interesting to note that a recent increase in on-farm growing of maize silage as cattle feed in southwestern England has, reportedly, increased the numbers of Starlings wintering in these areas, though impacts on breeding numbers are unknown (C.J. Feare pers. comm.).

The main prey of Starlings are soil- and ground-

	LRT							
Habitat/spatial split	$\chi^2$ df		Р	Parameter	Estimate	Interpretation		
None ( <i>n</i> = 246)	1192	1	< 0.001	Year	-0.037 (0.001)	Significant linear decline over time.		
Farm type (n = 51, 96, 185)	7.2	2	< 0.028	Arable	-0.011 (0.006)	Steeper decline on pastoral and mixed farms.		
				Mixed	-0.029 (0.002)			
				Grazing	-0.026 (0.002)			
Region (n = 40, 57, 79, 24, 34)	59.0	4	< 0.001	Southeast	-0.050 (0.002)	Significant declines in all regions, steepest in Southeast followed by North and West.		
				Fast	-0 025 (0 003)			
				Southwest	-0.034 (0.004)			
				West	-0.040 (0.003)			
				North	-0.042 (0.003)			
Geographic location (n = 684)	43.5	2	< 0.001	Year × latitude	-0.049 (0.008)	Declines tend to be steeper in the North and in the West.		
				Year × longitude	0.045 (0.012)			
Buildings (n = 284, 47)	0.29	2	ns	-		No difference in trends.		
Altitude ( $n = 702$ )	25.6	1	< 0.001	Year × altitude	0.0001 (0.0001)	Declines tend to be steeper at lower altitudes.		

 Table 3. Results of tests for linear declines in House Sparrow numbers on CBC plots with respect to different habitat and spatial divisions.

Significance of trends was tested using likelihood ratio tests (LRTs) and the parameter estimates  $(\pm 1 \text{ se})$  for the appropriate terms, on the log scale, are given, together with a brief interpretation of the results.

dwelling invertebrates, particularly leatherjackets (tipulid larvae) and earthworms, though they take a wide range of other taxa and some plant material, particularly in autumn (Kluijver 1933, Tinbergen 1981). There is little information published on population trends in Tipulidae and numbers are quite variable from year to year, making trends difficult to discern (Wilson et al. 1999). Biomass of soil invertebrates generally, and tipulids in particular, is highest in areas of permanent pasture, where soil disturbance is minimal (Paoletti 1999). Foraging birds are strongly associated with areas of pasture, particularly those with high densities of invertebrates (Tucker 1992, Whitehead et al. 1995, Feare 1994, Bruun 2002). Birds also find foraging in shorter swards easier, as they have to spend less time being vigilant, and can move more freely (Devereux et al. 2004).

The area of permanent pasture in Britain has decreased by two million hectares (5%) since 1965, which would have reduced the area of available foraging habitat. Also the use of insecticides on grassland, though low, is targeted partly at tipulids, which may have reduced foraging opportunities further (Vickery *et al.* 2001). However, the total area decline tells us relatively little. Some knowledge of the spatial patterning of this change, and how this relates to the distribution of Starlings, would be required to fully determine the importance of this loss of habitat in driving the population decline. For example, fertilizer usage on farmland has increased markedly, increasing sward height and density, and field drainage was particularly extensive in the 1970s, both of which may lead to reduced foraging opportunities, particularly during the breeding season (Chamberlain *et al.* 2000).

Relatively little is known about Starlings, or many other species, in towns and cities (Robinson et al. 2002a, Bland et al. 2004). The BBS results, presented here, reveal just how important suburban habitats are for Starlings, with almost 60% of the population present in garden/urban habitats. The number of Starlings using gardens in winter is also declining (Robinson et al. 2002b), but the causes for this are unclear, and may only reflect a shift in habitat use. Nesting attempts in urban and suburban areas tend to produce fewer young than those in more rural situations (Siriwardena & Crick 2002) and some starlings may not breed every year (Feare 1984). Nestsite availability in these habitats is unknown. Further research into urban Starling population dynamics is to be encouraged if we are to fully understand the causes of decline of this charismatic species.

In summary, Starlings have decreased in both woodland and farmland habitats in the wider countryside, which may reflect changes in the farming landscape.

Figure 2. Temporal trends in Starling population on different types

Information about the wintering population is fragmentary and numbers are difficult to quantify as Britain forms a continuous part of a European wintering range and Starlings are highly mobile both within and between winters (Feare 2002). However, Easterbrook (1999) recorded a 50% decline in wintering numbers in

Oxfordshire farmland and Robinson et al. (2002a) note that numbers using urban gardens in winter appear to be declining, though this does not appear to be true

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address this issue.

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for rural gardens. Co-ordinated counts of breeding populations across Europe may be the only way to

#### **ENDNOTES**

a. We fitted GLMs using the GENMOD procedure of SAS and compared models using likelihood ratio tests (SAS Institute 1996). Confidence intervals were derived from the analytically estimated standard errors produced by SAS. GAMs were fitted using the program GAIM (Hastie & Tibshirani 1990), models being fitted using ten degrees of freedom (recommended by Fewster et al. 2000) to produce smoothed trends. Confidence intervals were calculated by bootstrapping from a matrix of 199 replicates generated from re-runs of each model on new samples generated by resampling survey sites with replacement.

Both the GLM and GAM analyses of CBC data modelled number of birds counted as a function of a categorical plot effect and year, the latter being parameterized as either a categorical variable or as a continuous (parametric or nonparametric) predictor. Further predictor variables or interactions between these variables were introduced to make specific comparisons or to test hypotheses.

To identify significant turning points in the smoothed CBC and Garden Bird Feeding Survey trends, we employed the methods of Siriwardena et al. (1998) and Fewster et al. (2000), slightly adapted to consider changes in population growth rate rather than in abundance. Thus, we estimated the second derivatives (rates-of-change of the rate-ofchange) of the population trends in each year (on the log scale), together with their 95% confidence intervals, using the smoothed GAM trends and the matrix of 199 bootstrapped replicates of these trends. Years where the 95% confidence

of farmland as measured from CBC (a) arable, (b) mixed and (c) grass farms. Details as in Fig. 1.



interval of the second derivative did not overlap zero could be considered to be years in which there was significant curvature in the original trend being analysed (Siriwardena *et al.* 1998, Fewster *et al.* 2000). These turning points then provided both an intrinsically useful tool for describing trends and an objective means of dividing the population index time series into units with homogenous trends (Siriwardena *et al.* 1998, Fewster *et al.* 2000).

b. The regions were defined as follows. East: Hertfordshire, Bedfordshire, Northamptonshire, Nottinghamshire, Humberside and eastwards; North: Merseyside, Manchester, South Yorkshire and areas to the north; West: Gloucestershire, Warwickshire, Leicestershire, Derbyshire, Cheshire and areas to the west; Southwest: Avon, Wiltshire, Dorset and areas to the west; Southeast: London, Buckinghamshire, Oxfordshire, Berkshire, Hampshire and areas to the south and east.

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