Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain

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Summary

1. In Britain, the song thrush *Turdus philomelos* is categorized as a species of high national conservation concern because of a large population decline during the last three decades. We calculated a series of annual national population estimates for woodland and farmland habitats combined for the period 1964–2000. We then used turning points analysis to identify seven blocks of years within the period of decline (1968–2000) with uniform rates of population change in the smoothed trend.

2. We used recoveries of song thrushes ringed as nestlings, juveniles and adults during April–September to estimate survival rates separately for the post-fledging period, the remainder of the first year and for adults. Daily survival probability was lower during the post-fledging period than during the remainder of the first year or for older birds.

3. There was evidence for variation in survival rates among blocks of years with different rates of population change, particularly for first-year survival. There were significant positive correlations across blocks between mean population multiplication rate (PMR) and both post-fledging and first-year survival.

4. Survival of first-year birds was correlated negatively with the duration of the longest run of frost days and the survival of adults was correlated negatively with the duration of the longest summer drought. Variation among blocks in mean PMR was correlated with block means of the duration of runs of frost days and drought days, but significant correlations between PMR and both post-fledging and first-year survival remained after allowing for the influence of weather on survival.

5. Changes in survival in the first winter, and perhaps also the post-fledging period, are sufficient to have caused the song thrush population decline. The environmental causes of these changes are not known, but changes in farming practices, land drainage, pesticides and predators are all candidates. Adverse weather conditions contributed to the decline, but were not the primary driver.

Key-words: demographic models, juvenile mortality, population change, ringing recoveries, survival rates.

Introduction

In Britain, the song thrush (*Turdus philomelos* Brehm) is distributed widely across lowland habitats, with most birds occurring on farmland (36%), woodland (24%) or human-associated (24%) habitats (Gregory & Baillie 1998). However, a prolonged population decline reduced breeding densities on farmland by 69% between 1968 and 1999 (95% confidence limits 60–76%) and by 46% (30–58%) in woodland (Baillie et al. 2002). There is also evidence for a sustained decline in the number of birds feeding in gardens in winter (R. J. W. Woodburn et al. unpublished). The breeding population of song thrushes in Britain shows some local dispersal and seasonal movement, but only a small proportion of birds move outside Britain during the winter (Thomson 2002).
Thomson, Baillie & Peach (1997) investigated the demographic mechanisms of the decline by estimating annual survival rates of first-year and adult song thrushes using national ring recoveries. However, they were forced to assume that reporting rates of birds found dead did not vary with either age or year, as they did not have access to annual totals of the numbers of birds ringed in each age class. Furthermore, although they estimated the survival of birds ringed as independent juveniles, they did not estimate survival rates during the period between a young bird leaving the nest and becoming an independent juvenile, i.e. post-fledging survival, when mortality is likely to be high.

In this paper, we extend the analyses of Thomson et al. (1997) in five ways. First, we estimate the population trajectory of the combined song thrush population of woodland and farmland during the period 1964–2000 and then use recently developed analytical methods (Fewster et al. 2000) to identify blocks of years separated by turning points when the annual population multiplication rate (PMR; the ratio of population size in one year to that in the previous year) changed significantly. Secondly, we use methods developed by Thomson et al. (1999) to estimate survival during the post-fledging period, as well as for the remainder of the first year and for adult birds. Thirdly, we use newly available data on the numbers of birds ringed in each age class to explicitly model variation in reporting rate with respect to time and age. Fourthly, having obtained estimates of survival rates for all three age classes and all blocks of years, we use them in combination with the population trajectory to estimate mean productivity (young reared per adult per year) for each block. Finally, we assess the relative contributions of variation in productivity and post-fledging, first-year and adult survival as mechanisms driving population change.

Methods

POPULATION TRENDS AND TURNING POINTS

Farmland and woodland populations of song thrushes in Britain have been monitored by the British Trust for Ornithology’s (BTO) Common Birds Census (CBC) since its inception in 1964 (Baillie et al. 2002). Each year around 200 survey plots were visited 10–12 times by volunteers during the breeding season and the locations of all birds (mostly singing males) recorded on maps, which were then analysed using standard methods (Marchant et al. 1990) to give the total number of territories on each plot. Annual indices of population size were obtained from log-linear Poisson regression models with plot and year main effects (Pannekoek & van Streijn 1996; Peach, Siriwardena & Gregory 1999).

To estimate song thrush population changes in lowland rural Britain, we combined CBC indices for woodland and farmland habitats. We were unable to incorporate population data for song thrushes living near human habitations because monitoring in these habitats has begun only recently. During 1996–2000, about 20% of ringing records come from suburban habitats; such birds could not be excluded because ringing data has included habitat details only in recent years; hence, it was necessary to accept the slight mismatch in habitat coverage. There was little geographical mismatch between the population size and ringing data because the distribution of volunteer bird ringers is broadly comparable to that of CBC fieldworkers.

To calculate song thrush population size in farmland and woodland, CBC index values (Baillie et al. 2002) were standardized to a value of 1 in 1989 for each habitat. We then calculated the mean density of song thrush territories in farmland and woodland from CBC data for 1989, after excluding a small number of plots following Marchant et al. (1990). We multiplied the density of territories by the habitat area in 1989 and multiplied the entire CBC index series by this number. This was conducted separately for farmland and woodland, and the two series summed to give an overall estimate of population size. The relative numbers in each habitat were similar to those derived by Gregory & Baillie using a line-transect method (1998). The combined population size-time series was then smoothed using a thin-plate spline with 10 d.f. in SAS PROC TPSPLINE (SAS Institute 1997), following the recommendations in Fewster et al. (2000). We replicated this procedure 199 times by resampling (with replacement) the CBC plots and the central 95% of values were taken as the confidence interval for each year.

To identify periods during which annual PMRs were consistent, we used a modification of the turning points method of Siriwardena et al. (1998) and Fewster et al. (2000). Logarithms of the smoothed annual population estimates from each bootstrap replicate were taken and the second derivatives of the curve calculated for each year. Second derivatives that were significantly different ($P < 0.05$) from zero were considered to be turning points in the rate of population change, with each period of similar PMR delineated by these points constituting a block. We used logarithms of the smoothed series rather than the untransformed smoothed series so that the turning points identify a significant change in the proportional rather than absolute rate of change of the population.

RINGING AND RECOVERY DATA

About 2000 licensed volunteer ringers ring song thrushes in Britain throughout the year. During our study period about 1000–2000 birds were ringed annually as nestlings and about 6000 full-grown birds were ringed after being caught in nets and traps. Although the ringing scheme operates in both Britain and Ireland, a negligible proportion (c. 2.5%) of birds were ringed in Ireland. Survival rates were estimated from recoveries, i.e. ringed birds found dead and reported to the ringing scheme.

Most full-grown birds ringed during this period could be aged in the hand as being either juvenile (< 1 year
old) or adult (> 1 year old) using criteria given by Svensson (1992). Some birds ringed in winter are likely to have been migrants from breeding populations elsewhere in Europe (Thomson 2002); to exclude as many as possible of these we included only full-grown birds ringed between 1 April and 30 September. Recoveries of dead birds ringed during 1968–99 (the years for which numbers ringed were available in computerized form) and reported before 31 May 2000 were included in the analysis. We excluded from the analysis a small number of records relating to uncertain or unusual ringing or recovery circumstances, birds ringed while sick or injured and nestlings that were subsequently found dead in the nest, following criteria listed in Baillie & McCulloch (1993). In total, 2714 recoveries from 172 799 birds ringed in 32 cohorts were considered.

For birds ringed as nestlings three classes of age at recovery were defined: post-fledging, first-year and adult. Post-fledging recoveries were taken to be those occurring within 63 days of the date of ringing of nestlings, which represented the difference between the median dates of ringing of nestlings and of full-grown young in their first year (Fig. 1). This will include some nestling mortality, as birds are ringed typically 4–5 days before fledging; mortality due to whole brood losses will be around 0·10 in this time (Paradis et al. 2000). Recoveries between 63 days after the ringing of nestlings and 31 May in the following year were classed as being of independent first-year birds. Recoveries after this date were classed as being of adult birds. Birds ringed as juveniles were recovered as first-years if the recovery occurred before 31 May in the year following hatching, after which they were classed as being recovered as adults. Birds ringed as adults and recovered before 31 May the following year were classed as having been recovered in the year of ringing. Subsequent recovery periods ran from 1 June to the following 31 May, reflecting the median ringing date of adult birds (Fig. 1). The length of the recovery period in the year of ringing for birds ringed as juveniles and adults varied because ringing occurred over a period of months. However, the distribution of ringing dates within the ringing period did not change substantially between years, so is unlikely to bias our survival estimates (Smith & Anderson 1987).

**ANALYSIS OF SURVIVAL RATES**

The methods follow Thomson et al. (1999) and are an extension of the approach of Brownie et al. (1985). For birds ringed as nestlings, the expected proportions (k) recovered in each period are defined as:

\[
\begin{align*}
    k_{\text{post-fledging}} &= (1 - \phi_{\text{pf}}) \times \lambda_{\text{pf}} \\
    k_{\text{first-year}} &= \phi_{\text{pf}} \times (1 - \phi_{\text{fy}}) \times \lambda_{\text{fy}} \\
    k_{\text{adult (2nd year)}} &= \phi_{\text{pf}} \times \phi_{\text{fy}} \times (1 - \phi_{\text{ad(2)}}) \times \lambda_{\text{ad(2)}} \\
    k_{\text{adult (3rd year)}} &= \phi_{\text{pf}} \times \phi_{\text{fy}} \times \phi_{\text{ad(2)}} \times (1 - \phi_{\text{ad(3)}}) \times \lambda_{\text{ad(3)}}
\end{align*}
\]

where \( \phi \) denotes survival probability and \( \lambda \) reporting rate (i.e. proportion of birds dying in a period that are reported), and the subscripts refer to the different age-classes. The equivalent expected proportions for birds ringed as juveniles and adults are similar in structure and identical to those of Brownie et al. (1985).

All survival models were fitted using the software package MARK (White & Burnham 1999) with logit link functions. Models were specified in terms of survival probability (\( \phi \)) and reporting rates (\( \lambda \)), which could differ among age-classes and among calendar years, with subscripts used to identify model parameters. Lower case letters indicate categorical variation in parameters; for example, \( \phi_a \) means that survival is different for each of the three age related recovery periods (a) and also differs independently among calendar years (t), i.e. with \( 3 \times 32 = 96 \) parameters. Upper-case
letters indicate linear trends (on the logit scale). For example, \( \lambda_{at} \) means that each age class has a different logit-linear trend in reporting rate with time in years since the beginning of the study period. As the first-year and adult (but not post-fledging) recovery periods overlap substantially, we considered models in which rates varied with time in a similar way but with fixed additive (in logit terms) differences in rate among the age classes. This was indicated by placing a '+' sign between the age-classes assumed to be varying in parallel across time. For example, \( \phi_{\text{fyf,yad}} \) means that survival is assumed to vary among calendar years, with variation during the post-fledging period being independent of that for the first-year and adult recovery periods, which are assumed to undergo parallel fluctuations with year.

The principal objective of the modelling was to test for temporal changes in the survival rates of each age-class and then to test for correlations between changes in survival rates and population size (from the CBC data). To avoid the latter being based upon relatively imprecise calendar year-specific estimates (with potentially high sampling correlations) we fitted models in which survival was assumed to vary among blocks of years (\( b \)) defined by the turning points analysis, but not to vary with calendar year within these blocks (model \( \phi_{a} \)).

In addition to age-specific and fully time-dependent models of reporting rate, we considered models with different logit-linear declines in reporting rate for each age class, because systematic temporal declines in reporting rates have been found for other species (Baillie & Green 1987; Catchpole et al. 1999). We also fitted models with first-year and adult reporting rates varying in parallel and a model with annual variation in reporting rate for adult and first-year birds superimposed on a linear trend (\( \hat{\lambda}_{at} \)).

We used Akaike’s information criterion (AIC; Anderson, Burnham & White 1994) to identify parsimonious models that accounted for important sources of variation in the data while fitting as few parameters as possible. In fitting the global model \( \phi_{a} \lambda_{a} \) (i.e. one with a separate survival and reporting rate for each age class and year, a total of 189 estimable parameters), some over-dispersion was noted (the over-dispersion parameter \( \hat{c} = 1.99 \)). This is not unusual in ecological studies, where values of \( \hat{c} \) between 1 and 3 might be expected. Consequently, we report a quasi-likelihood version of the AIC, the QAIC; parameter estimates are unaffected by this, but variances are inflated by \( \hat{c} \).

**Survival and Weather**

Previous studies have shown that weather, particularly during winter, can affect song thrush survival (Baillie 1990; Thomson et al. 1997). Earthworms and other soil-dwelling invertebrates form a large component of the diet of song thrushes, particularly between December and May (Davies & Snow 1965). Earthworms move deeper into the soil and/or become inactive during periods of dry or cold weather and hence become less available as prey for song thrushes. Dry summer soil conditions are associated with reduced consumption of earthworms by song thrushes, increased consumption of snails and spiders and reduced body condition in chicks and adults (Davies & Snow 1965; Gruar, Peach & Taylor 2003). Thus, periods of prolonged drought in summer and cold weather in winter might increase song thrush mortality by reducing the availability of food. Cold winter weather will also impose an increased thermoregulatory burden.

We extracted daily temperature and rainfall data for three stations in England selected to give broad regional coverage of lowland areas (where most song thrushes are ringed): Rothamsted, Hertfordshire (51°48’N 0°21’E, 128 m asl); Long Ashton, Somerset (51°26’N 2°40’W, 51 m asl) and Cockle Park, Northumberland (55°13’N 1°41’E, 95 m asl). For each station, we calculated the length of the longest period of consecutive frost days (mean air temperature < 0 °C) between October and March and consecutive drought days (total daily rainfall < 1 mm) between June and mid-August. The number of consecutive frost days and drought days were then averaged across the three stations. These weather time-series were correlated strongly between Rothamsted and Long Ashton (\( r > 0.9 \)), but less strongly between these two stations and Cockle Park (\( 0.5 < r < 0.7 \)). Models in which survival rates were assumed to depend logit-linearly on winter frost or summer drought duration were denoted with subscripts F and D, respectively.

We simplified the weather model of survival (starting from \( \phi_{\text{fyf,yad}} \lambda_{\text{aF,D}} \)) in a ‘step-down’ fashion, using likelihood ratio tests to assess the significance of removing each linear relationship in turn until no further terms could be removed without significantly increasing the residual deviance. Reporting rate was modelled throughout as \( \hat{\lambda}_{at} \), the most parsimonious formulation across a range of survival models (Table 1).

**Season-long Productivity**

We were unable to estimate directly all the demographic rates necessary to model song thrush population change. We estimated survival rates of fledging and full-grown birds from ring recoveries (see above) and we assumed that all birds aged 1 year and older attempt to breed each year. Hence, the population of breeding birds \( N \), as surveyed by the CBC-based method, in year \( i \) + 1 is related to the population in the previous year by:

\[
N_{i+1} = N_i \times (\phi_{\text{ad}} + P \times \phi_{\text{phi}} \times \phi_{\text{fy}}),
\]

where \( P \) is the mean number of young reared to ringing age per adult per year and the \( \phi \) are year- and age-specific survival rates. We therefore used the CBC-based population change data to estimate the average value of \( P \) within the blocks of years defined by the turning points analysis, by first estimating the average PMR.
within a block of years beginning in year i and ended in year j, PMR\(_{ij}\) as:

\[
PMR_{ij} = \frac{N_j}{N_i} \left( \frac{1}{j-i} \right)
\]

where \(N\) represents the song thrush population estimates in years i and j from the smoothed CBC trajectory. The average breeding productivity \(P\) in the block was then estimated from PMR\(_{ij}\) and the block- and age-specific estimates of survival (\(\phi\)), by rearranging eqn 2 as:

\[
P_{ij} = (PMR_{ij} - \phi_{ad(ij)})/(\phi_{pf(ij)} \cdot \phi_{fy(ij)})
\]

**Table 1.** Modelling of reporting rate with various assumptions about age and time dependence of survival rates. Column gives \(\Delta QAIC\) (i.e. QAIC relative to that of the best model) for each reporting rate model (\(\lambda\)) under various different scenarios for survival rates (\(\phi\)); for each example of survival the most parsimonious model is given in bold. The number of parameters (NP) used in each formulation is also indicated; for details of model specifications, see text

<table>
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<tr>
<th>NP</th>
<th>(\lambda_{ad})</th>
<th>(\lambda_{pf(y+ady)})</th>
<th>(\lambda_{pf(y+ady)})</th>
<th>(\lambda_{pf(y+ady)+t})</th>
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<td>82·4</td>
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**Results**

**POPULATION TRENDS**

Following a rapid recovery from the cold winter of 1962–63, the song thrush population declined continuously between 1968 and 1998 (Fig. 2). Turning points analysis on the smoothed trend line for 1968–2000 divided the series into seven blocks, the first six of which reflected declining abundance; only the most recent block (1998–2000) shows a modest recovery in numbers. The most rapid decline occurred in the late 1970s.

**REPORTING RATES**

The most parsimonious description of reporting rates was a logit-linear temporal decline with different slopes and intercepts for all three age-classes (Table 1). Sampling correlations between the reporting rate estimates were relatively high (0·50 < \(\beta\) < 0·85) and models with the same juvenile and adult reporting rates had only marginally (\(\Delta QAIC < 2\)) higher QAICs. The temporal decline in reporting rate was slightly greater for birds that died as adults (change in log odds per year \(\beta = -0·063 \pm 0·007\) (SE), from model \(\phi_{ad}\), \(\lambda_{at}\)) than for juveniles (\(\beta = -0·047 \pm 0·017\) and the temporal decline in reporting rate for birds that died during the post-fledging period was least marked and not significant (\(\beta = -0·010 \pm 0·012\)). Similar estimates of reporting rate trends were obtained under alternative survival rate formulations and, in each case, the \(\lambda_{at}\) model had the lowest QAIC (Table 1). Adult and juvenile reporting rates have declined from around 3% in the late 1960s to 0·5% and 0·8%, respectively, whereas post-fledging reporting rate has remained around 1·5%. Because the \(\lambda_{at}\) formulation was the most parsimonious for all definitions of survival investigated, we restricted our evaluation of temporal changes in survival to this formulation of reporting rate.

**VARIATION IN SURVIVAL**

Average daily survival (from \(\phi_{at}\), for median recovery periods) was lower during the post-fledging
period ($\phi_{yl} = 0.9844$) than during the remainder of the first year ($\phi_{yl} = 0.9980$) or subsequent adult years ($\phi_{ad} = 0.9987$). This pattern was consistent across models, irrespective of the way in which calendar year or block effects were defined. Survival rates varied among blocks (Fig. 3), but only in the case of first-year survival was this variation statistically significant (LRT test: $\phi_{yl\lambda T} vs. \phi_{ad\lambda T}\lambda_{T}, \chi^2 = 25.9, P = 0.0002$).
and this was the most parsimonious model of those tested.

In the starting model that included all five of the weather related survival effects \( \phi_{D(pf,fy,ad)}F(fy,ad) \), the estimated coefficients all had the expected negative sign (one-tailed sign test: \( P = 0.031 \)). All sampling correlations between these parameters were \( |r| < 0.1 \). However, this model could be simplified to \( \phi_{a(pf)},D(ad),F(fy) \) in which there were significant negative effects of the duration of winter frosts on the survival rate of first-year song thrushes (\( \beta = -0.061 \pm 0.023 \)) and significant negative effects of the length of summer drought on adult survival (\( \beta = -0.017 \pm 0.008 \)); other effects of weather on survival were not statistically significant when added to this model.

Correlates of variation among blocks in the rate of population change

PMR appeared to be correlated with the survival of birds in their first year, both in the post-fledging stage and the remainder of the year (Fig. 4). Both of these correlations were influenced strongly by the sixth (short) block (1998–2000) when the population increased and survival was estimated with relatively low precision. When this block was omitted, the correlation between PMR and \( \phi_{pf} \) became nonsignificant (\( r = 0.41; P > 0.2 \)) but that for \( \phi_{fy} \) remained significant (\( r = 0.77; P = 0.04 \)).

Comparing correlations between observed block-specific PMRs and EPMRs under different combinations of time-varying demographic rates suggests that variation in post-fledging and first-year survival rates contributed to the observed rates of population change, but that productivity and adult survival did not (Table 2). Removing block-specific variation in post-fledging and

Table 2. Effect on expected population multiplication rate (EPMR) of variation among time blocks (see text) of demographic parameters. EPMR was calculated as described in the Methods, and Pearson’s \( r \) correlations between this and the observed PMR values for each block were calculated, with survival rate parameters varying between blocks (b) or constant across blocks (c). Although the significance of \( r \) cannot be assessed in the conventional sense, for reference the 95% limit for \( r \) is 0.754. Note that \( r \) for the model with all rates block-specific must be 1.000 because of the way the rates are estimated.

<table>
<thead>
<tr>
<th>Model</th>
<th>( P )</th>
<th>( \phi_{pf} )</th>
<th>( \phi_{fy} )</th>
<th>( \phi_{ad} )</th>
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</table>

Fig. 4. Relationship between population multiplication rate (PMR) and demographic rates for the seven blocks defined by turning points analysis. PMR was calculated from the smoothed index within periods with consistent rates of population change (see Fig. 2), block-specific survival rates (± 1 SE) come from model \( \phi_{D,ad},F(fy) \) and productivity from the population model (see text). Correlations of demographic rates with growth rate: \( P r = -0.73, NS; \phi_{pf},r = 0.87, P < 0.05; \phi_{fy},r = 0.90, P < 0.01; \phi_{ad},r = 0.25, NS. \)
first-year survival removed the correlation between observed and expected PMR, conversely introducing time variation in these rates when the others were assumed constant greatly increased the degree of correlation.

Block-specific PMRs were correlated negatively with block means of summer drought and frost duration (Fig. 5). However, these weather variables alone did not seem to account entirely for the relationship between survival and PMR. The correlations between block-specific PMRs and the weather-adjusted survival estimates (Fig. 6) were similar to those observed without allowing for weather effects (Fig. 4). There was a strong

correlation between PMR and EPMR generated from a model with these weather-adjusted age- and block-specific survival estimates and constant productivity $P$ ($r = 0.849$). Similar results were obtained when the adjustment of survival was made using only the statistically significant effects of weather (frost duration on first-year survival and drought duration on adult survival). Hence, although weather variability has exacerbated particular periods of decline, it seems unlikely to have driven the decline.

Discussion
The song thrush, in common with a number of other passerine species that occur widely on farmland, has experienced a large population decline since the 1970s (Baillie et al. 2002). The analyses presented here suggest that changes in survival of birds in their first year of life after fledging have had the greatest impact on population changes. These conclusions largely support those of Thomson et al. (1997), but extend those results by highlighting the potential importance of changes in post-fledging survival. We also show the necessity of modelling reporting rates explicitly in rigorous analysis of large-scale ringing data; one cannot assume such rates are constant. This is likely to be the case for many species (Baillie & Green 1987; Dunn 2001).

The Importance of Post-Fledging Survival
This is one of the first studies of post-fledging survival at a sufficiently large spatial scale that failure to detect surviving birds caused by emigration can be disregarded as a cause of apparent mortality. It should be noted that our definition of the post-fledging period was imposed by the nature of our data (the difference in median ringing dates of nestling and first-year birds, Fig. 1) and not biological (e.g. the period of dependence). Daily post-fledging survival estimates show a positive correlation with the duration of the period over which survival was measured, indicating that daily survival rates increased with time since fledging (Fig. 7). For example, Thomson & Cotton’s (2000) estimate of daily post-fledging survival was much lower than ours, but was measured over a much shorter period (14 days from fledging). This finding indicates that comparisons of post-fledging survival among species or studies must standardize or otherwise allow for the period over which it is measured.

Although survival during the post-fledging period was low compared to that of older birds, it was similar that recorded from other passerines (Fig. 7), and this does not necessarily imply a large impact on population trend. Given the observed average survival rates (from $\phi, \lambda$, our population model (eqn 2), suggests a productivity of 1.86 fledglings per bird per season (or 3.72 fledglings per pair) are required to maintain a stable population. Successful song thrush breeding attempts in Britain fledge an average of 3-69 young (Paradis et al. 2000), so each pair would need to fledge an average of only one brood per season for the population to remain stable. Because female song thrushes in Britain typically lay several clutches in a season of which an average of 44% produce fledged young (Paradis et al. 2000), such productivity seems plausible. Furthermore, changes in post-fledging survival have the opportunity...
to be compensated for by density-dependent changes in demographic rates that occur later in the life history.

**DID CHANGES IN WEATHER CAUSE THE SONG THRUSH POPULATION DECLINE?**

We found a significant negative effect of cold winter weather on the survival of song thrushes in their first year and a significant negative effect of summer drought on the survival of adults. Thomson *et al.* (1997) found negative effects of cold winters on the survival of first-year and adult song thrushes. Variation in weather conditions influenced survival and the mean PMR of a block was correlated with block means of frost and drought duration. However, these effects did not account for the differences in PMR among blocks. When we adjusted the block-specific estimates of survival to those expected if weather conditions had remained constant throughout the study period, we still found a strong correlation between observed PMR and adjusted post-fledging and first-year survival rates.

Further evidence that the effects of weather did not fully account for the decline of the song thrush population is apparent in plots of annual population changes against frost and drought duration (Fig. 8). It can be seen that the population tended to increase more in 1964–68 than would be expected from the relationship of PMR to weather conditions from 1968 onwards. First-year survival of song thrushes may have been unusually high in this period (Thomson *et al.* 1997). It seems likely that the song thrush population grew rapidly during 1964–68 because of a density-dependent response to low population size caused by the abnormally cold 1962/63 winter and that first-year survival rates may have been at least part of the mechanism of density-dependence. However, the low PMR values in the period 1978–2000, when the song thrush population was lower than during the period of rapid increase,
indicate that the nature of any density-dependent relationship changed markedly in the 1970s.

OTHER ENVIRONMENTAL CORRELATES OF POPULATION DECLINE

The pattern of song thrush population change resembles closely that of bird species associated more strongly with farmland (Fuller 2000). In recent decades, agricultural practice in Britain has changed markedly as intensification of production has increased. The greatest changes occurred in the periods 1970–74 and 1982–88 (Chamberlain et al. 2000). Although the number of song thrush territories is generally greater in farmland than woodland areas, most territories and foraging tend to occur in non-cropped habitats, particularly damp field boundaries, woodland edge, scrub and gardens (Mason 1998; Peach et al. 2002). Grazed permanent grassland is also an important foraging habitat for song thrushes but most arable crops, particularly cereals, are avoided (Buckingham et al. 2002; Peach et al. 2002).

Two major changes in agricultural land use that are likely to have had negative impacts on farmland song thrushes are hedgerow removal, with loss rates highest between 1978 and 1990 (Barr et al. 1993) and the conversion of permanent grassland to arable cultivation with under-field drainage which peaked during the late 1970s facilitated by the availability of government grants (Robinson & Armstrong 1988). Earthworms are generally much more abundant in permanent grass fields than in arable fields, due probably to the damper soil conditions, higher levels of organic matter and absence of ploughing and pesticide application on grass (Tucker 1992; Edwards & Bohlen 1996). Snails also form a large part of the prey of song thrushes, particularly when other food is scarce (Davies & Snow 1965; Gruar et al. 2003). Large increases in the usage of molluscicides on farmed land (Garthwaite & Thomas 1996) and gardens may have reduced prey availability for song thrushes or possibly caused direct mortality through secondary poisoning, although their use tends to be greatest during wet summers, when prey availability is at its highest.

Song thrushes are frequent prey of sparrowhawks (Accipiter nisus L.) and Thomson et al. (1998) found that it was the only one of 12 declining passerine bird species in Britain for which there was a significant tendency for populations to change more negatively on CBC plots following the arrival of sparrowhawks. However, there is no evidence of a negative relationship between block-specific post-fledging and first-year survival rates of song thrushes and block-specific means of the CBC index for sparrowhawk (Baillie et al. 2002). Paradis et al. (2000) found that large-scale spatial variation in the nest success of song thrushes was negatively correlated with the abundance of corvids, which are predators of eggs and nestlings. Stoate & Szczur (2001) found that nest success and breeding populations increased markedly following the introduction of predator control to a farm in lowland England, though changes in habitat management may also have influenced population size. However, the absence of any correlation between PMR and productivity and increasing average nest success rates over time (Baillie et al. 2002) suggests that increases in nest failure rates due to increased corvid densities are an unlikely cause of the national population decline.

THE ROLE OF DENSITY DEPENDENCE

First-year survival rates were significantly lower during the two periods of steep population decline (c. 48%) than during the periods of relative population stability (60%, Fig. 3). This suggests that song thrush population dynamics are density-dependent, i.e. a given change in the environment is likely produce only a transient change in the relevant demographic parameter, not a long-term trend in it, which would yield an ever-accelerating population decline (Green 1999). In general, birds in their first year of life are known to suffer in competition for resources (Wunderle 1991), particularly during periods of environmental stress such as prolonged frosty weather, when soil invertebrates are likely to be unavailable as prey. Rates of population decline were particularly high during periods with relatively severe winters, when first-year survival is low.

The pattern of density-dependent processes need not have been constant over time. Thus, for example, song thrush populations recovered quite quickly from an external environmental stress in the early 1960s (a harsh winter) but were, apparently, unable to do so after steep declines in the 1970s and 1980s. Populations of many farmland resident birds (but not summer migrants) have shown the greatest declines at similar times as the song thrush, i.e. the late 1970s and mid-1980s (Siriwardena et al. 1998) and many of them have also shown few signs of subsequent recovery, despite at least some having shown significant population increases after the 1962/63 winter. This would be consistent with the generally deleterious impact of agricultural change on much of the UK landscape (Chamberlain et al. 2000; Robinson & Sutherland 2002), being exacerbated by periods of environmental stress. The changing nature of the density dependence and the inability of these populations to recover their former numbers may have consequences for the successful implementation of the UK government’s Public Service Agreement to reverse the population declines in British farmland birds by 2020 (DETR 1999).

Conclusions

Changes in demographic parameters do not need to be large or sustained to produce marked changes in abundance. Nevertheless, we provide clear evidence that reduced survival of first-year birds has been sufficient to account for the decline in numbers of song thrushes.
breeding in Britain. Furthermore, we have shown that while survival is correlated with weather conditions, these do not explain fully the long-term decline. It has not yet been possible to identify which of a range of other candidate environmental causes have been responsible for long-term changes in the abundance of song thrushes, due mainly to a lack of long-term data on the relevant environmental variables. Even if such data were available, correlations with underlying environmental changes might be obscured by lags, interactions with other variables or temporally varying density dependent processes. Future work needs to concentrate on improving our understanding of the relationships between survival and environmental variables.

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