Understanding the decline of the British population of Song Thrushes *Turdus philomelos*

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The British Song Thrush *Turdus philomelos* population has declined by 65% over the last thirty years. We describe the results to date of an integrated research programme, which aims to contribute ultimately to a recovery plan. We combined analyses of extensive long-term data sets from the British Trust for Ornithology (BTO) with intensive field studies on stable and declining populations. BTO data indicate no long-term decline in clutch size, hatching success, or fledging success of Song Thrushes (Baillie 1990), nor a substantial decline in adult annual survival rate. There is however evidence that first-year survival rates have declined enough to have driven the decline (Thomson *et al*. 1997). Post-fledging survival appears to be particularly low and may be the main component of this decline. Intensive field studies confirmed that clutch size, hatching success and fledging success are similar in stable and declining populations, whereas post-fledging survival seems low overall and poorer in the declining population. Birds in the declining population made substantially fewer nesting attempts per season. However, matrix models indicate that Song Thrush population growth rates are, *pro rata*, relatively insensitive to changes in seasonal breeding performance and most sensitive to changes in survival rates, particularly adult annual survival rate. When the matrix models were combined with the estimates of change in each vital rate, we found that seasonal productivity, post-fledging survival and first-year survival rates were all of similar importance, but adult annual survival rate appeared unimportant because it had not changed significantly.

The UK Song Thrush *Turdus philomelos* population has declined by over 65% since the mid-1970s (Baillie 1990, Marchant *et al*. 1990), with the biggest declines occurring on farmland (Fuller *et al*. 1995). The Song Thrush, along with many other common farmland breeding birds, is now red-listed as a species of high conservation concern (Gibbons *et al*. 1996). The causes of the decline are not however well understood. Although widely discussed (Fuller *et al*. 1991, Tucker 1992, Green *et al*. 1994, Saris *et al*. 1994, Fuller *et al*. 1995, Campbell *et al*. 1997), there is still only limited evidence that agricultural change has been the cause of the Song Thrush decline, and while Song Thrush populations are indeed affected by winter weather conditions, climatic change cannot account for the decline (Baillie 1990, Greenwood & Baillie 1991, Baillie 1993, Thomson *et al*. 1997). Increases in the number of Magpies *Pica pica* and Sparrowhawks *Accipiter nisus* may lower survival rates or nesting success, but there is little evidence for any persistent effect on the size of songbird populations (Gooch *et al*. 1991, Thomson *et al*. 1998).

In light of the Song Thrush population decline, and in the absence of an understanding of it, the Royal Society for the Protection of Birds (RSPB) and the British Trust for Ornithology (BTO) initiated a research project to study the population dynamics and ecology of the Song Thrush. The project recognizes that the list of possible environmental causes is long and seeks to narrow this list by studying firstly the demographic mechanism of the decline. The project integrates two types of research: analyses of changing demography using extensive long-term data held by the BTO, and an intensive comparative field study of Song Thrush ecology at two sites in southern England: one where numbers have been stable and one where they have declined. Here we provide an overview of the project to date.

OVERVIEW OF METHODS

Extensive study

Using data from the BTO Nest Record Scheme, Baillie (1990) began the process of studying long-term changes in Song Thrush demographic rates. He looked at whether clutch size had declined over the period 1962-88 and, using the Mayfield method (Mayfield 1961, 1975, Johnson 1979), he calculated daily egg and chick survival rates to test whether hatching and fledging success had decreased over the period 1962-1981. Assuming that reporting rates of dead adult Song Thrushes were constant between years within cohorts (*sensu* Aebischer 1987), he used ring-recovery data to estimate adult survival rates and look at whether they had declined between 1956 and 1985.

Baillie's (1990) work was followed up by Thomson *et al*. (1997) who investigated the survival rates of first-year birds as well as adults. Because of appreciable investment in a programme to computerise Song Thrush ringing data for the period 1977-1992, they were able to test more assumptions and fit more complex models (Brownie *et al*. 1985) than had previously been possible, using not just ring-recovery data, but also the ringing data themselves. Where the totals of birds of each age class ringed each year are thus known, it is possible to estimate both the survival rate and reporting rate in each year. Having thereby modelled reporting rates, and found no evidence that they varied with respect to age or time over this period, they used ring-recovery data for a more extensive period (1962-1993) to estimate survival rates using models that assume constant reporting rates within cohorts between consecutive years (Aebischer 1987).

Following further computerisation of Song Thrush ringing data for the period 1968-1977, current work is using new analytical software (White & Burnham 1999) and new models (Thomson *et al*. 1999) to address two issues in more detail. Firstly, we are looking at whether the declines in first-year survival rates reflect changes in post-fledging survival through the first sixty days, or survival through the remainder of the first year. Secondly, we are looking at whether the changes in survival rates are still apparent in models that control explicitly for patterns of variation in reporting rates. Further, we are using matrix models (McDonald & Caswell 1993) as a way of interpreting the importance of changes in each of the vital rates. With these we have calculated sensitivities and elasticities: the sensitivity is the absolute change in population growth rate resulting from an absolute change in a demographic rate, and the elasticity is the proportional change resulting from a proportional change in a demographic rate.

Intensive study

Fieldwork started near Graffham, West Sussex in 1995 and at Chipping Ongar, Essex in 1996. The Sussex site is predominantly pastoral, with some arable and mixed farming, and was chosen from a list of BTO Common Birds Census (CBC) plots for which long runs of data were available and on which the Song Thrush density had remained stable throughout the period of national decline. The Essex site is almost entirely arable and is centred on a CBC plot where numbers had declined in parallel with the national population. Both sites have an approximate area of 10 km^2.

Breeding-season fieldwork initially concentrated on productivity per pair and post-fledging survival. Analyses of long-term BTO data sets are unable to take account of possible changes in the number of nesting attempts made each season.

We followed individual pairs throughout the breeding season, recording the outcome of all nesting attempts. This research was restricted to intensively monitored areas (IMAs) within each study site to ensure that all breeding attempts were recorded. Within IMAs, all potential nesting habitat was searched frequently throughout the breeding season.

All pulli were individually colour-ringed. We used standardised searches on post-fledging day 14 to assess mortality following fledging. Recent research using radio-telemetry indicates that Song Thrush fledglings remain within 150 m of the nest until around 20 days post-fledging (Hill 1998), so fledgling numbers on day 14 are highly likely to reflect mortality rather than emigration.

OVERVIEW OF RESULTS

The principal findings of the intensive and extensive studies are summarised in Table 1.

Extensive study

Overview of published work

Baillie's (1990) work showed that the average clutch size of Song Thrushes had been constant through time, with no long-term trend nor appreciable fluctuations from year to year. He found that both hatching success and fledging success had actually increased slightly through time. His work therefore suggested that the population decline was not being driven by a fall in the success of individual breeding attempts. He also found no evidence of a decline in adult annual survival rate. By a process of elimination, these results suggested that the population decline was being driven either by a decline in first-year survival rates or by a change in the number of breeding attempts made by individual birds. At that time, because not all data were computerised, any estimates of first-year survival rates would have been conditional on the assumption that reporting rates within cohorts were constant with respect to both age and time.

Using newly computerised ringing data, Thomson *et al*. (1997) found no evidence that reporting rates varied significantly between years or between age-classes over the period 1977-1992. Assuming that reporting rates within cohorts were indeed constant between age-classes and between years, they found that adult annual survival rates had been relatively stable through time at an average of 0.571, showing only a slight increase followed by a slight decrease. By contrast, first-year survival rates showed a pronounced decline, falling from an average of 0.484 before

Table 1. Summary of estimates of change in each vital rate of the British Song Thrush population, from an extensive study based on 30 years of BTO national monitoring data, and from an intensive comparative study of sites with stable and declining numbers.

Vital rate	Extensive study	Intensive study
Clutch size	Stable at 4.1 eggs (Baillie 1990)	Similar clutch size at both sites (4 eggs)
Productivity per attempt	Slight increase: daily egg survival rose from 0.9615 to 0.9686 while daily chick survival rose from 0.9397 to 0.9461 (Baillie 1990)	Similar at both sites (3.3 chicks fledged per attempt)
No. nesting attempts per season	-	4 in the stable population, 2.5 in the declining population
Seasonal productivity	-	4.0 young per season in the stable population, 2.7 in the declining population
Post-fledging survival	Falling from 0.45 to 0.32 survival through the first 60 days	0.65 survival through first 14 days in stable population, less than 0.50 survival in declining population
First-year survival after post-fledging period	Some evidence of a decline parallel to that of post-fledging survival	-
Adult annual survival	Stable	-

the decline to 0.405 during it. Using a demographic model in which all other vital rates were held constant, they found that a change of this magnitude was large enough to account for the population decline.

Accordingly, they sought to follow up their findings in two ways. Firstly they aimed to look at whether changes had taken place in survival through the early (post-fledging) part of the first year, or in survival through the later part. Secondly, they sought to examine the assumptions about reporting rates in more detail with a further programme of data computerisation. Thomson *et al.* (1999) developed analytical models that could be used to address these issues.

Overview of current work in progress

We found that the rate of post-fledging survival through the first 60 days averaged only 0.405 (95% CI: 0.367-0.444), and the data indicate that the post-fledging survival rate has fallen linearly from 0.452 (95% CI: 0.399-0.506) in 1968 to 0.320 (95% CI: 0.250-0.399) in 1992. As well as the decline in post-fledging survival rate, we also found evidence of declines in survival through the remainder of the first year, and these patterns were apparent in models that included an explicit estimate of reporting rate in each year. Using Akaike's Information Criterion as a guide in model selection (White & Burnham 1999), four models with time-specific reporting rates described the data well - all included downward trends in post-fledging survival rate, but only three had a downward trend in survival through the rest of the first year. The evidence for a decline in post-fledging survival rate is thus stronger than the evidence for a decline in survival through the first year beyond that. However, neither can be fully distinguished from a combination of full temporal variation in reporting rates combined with separate temporal trends in the reporting rates of the different age-classes. When these more complex patterns of variation in reporting rate were included, the declines in survival were no longer significant. Estimation of large numbers of parameters in these complex models may simply be reducing the precision with which the survival rates are estimated. This may be obscuring patterns, but the possibility that variable reporting rates bias the estimates of survival rates in the simpler models cannot yet be ruled out. Further work aims to look at this in more detail.

Based on findings to date, the best estimates of change in each of the demographic rates are as follows. There is no evidence that adult annual survival rate has changed. Post-fledging survival rate and first-year survival rate have fallen in parallel by 0.132, and in proportional terms, these drops represent 32.6% of the mean post-fledging survival rate, and 28.5% of the mean first-year survival rate. If we can extrapolate the estimates of seasonal breeding productivity from the intensively studied stable and declining populations, and use these as measures of national productivity before and during the decline, they would represent a fall of 0.65 young per adult per year which is 38.8% of the average value.

Matrix models provide indications of the relative importance of changes in each vital rate. Here, they indicate that, *pro rata*, Song Thrush population growth rates are influenced most by changes in adult annual survival rate (sensitivity = 1; elasticity = 0.6130), and least by changes in breeding productivity per adult per year (sensitivity = 0.2356; elasticity = 0.3705). Post-fledging survival and subsequent first-year survival rates are intermediate with sensitivities of 0.8285 and 0.7033 respectively, and both share the same elasticity of 0.3705 (as for breeding productivity).

However, when we combine the results of matrix models with these estimates of change in each vital rate, patterns emerge that are not apparent from either one in isolation. Adult annual survival rate would cause no change in population growth rate, breeding productivity could achieve a 14% change in population growth rate, post-fledging survival rate could cause a 12% change, and first-year survival rate could achieve an 11% change. The high sensitivity of adult annual survival rate is cancelled out by its apparent stability, and the apparently large changes in breeding productivity are counter-balanced by low sensitivity.

Intensive study

Although of approximately equal area, the Essex site holds fewer than 50 breeding pairs of Song Thrushes compared with over 150 pairs in Sussex. Intensive monitoring has revealed major differences in the breeding success at the two sites. Clutch size and brood size at fledging are similar at the two sites and between years. Females lay, on average, clutches of 4 eggs, and the mean brood size for successful attempts is approximately 3.3. This agrees well with national BTO data that show no changes in clutch size and brood size over the past 30 years. Over 70% of nests at both sites fail to fledge young, largely owing to predation of eggs and chicks.

However, we found that the mean number of nesting attempts per pair was significantly lower in Essex. Song Thrush pairs in Sussex averaged approximately 4 nesting attempts per year compared with only 2.5 per pair in Essex. In Sussex, most Song Thrush pairs started to breed by mid March, and continued regular nesting attempts until July. There was no difference between Sussex and Essex in the date of first egg laying. However, in Essex many Song Thrush pairs showed prolonged time periods between successive attempts. As a result, there are significant differences in productivity per pair: in Sussex pairs fledged approximately 4.0 young per season, compared with around 2.7 in Essex.

Furthermore, the standardised searches revealed that survivorship to 14 days after leaving the nest was lower in Essex. Approximately 40% of nestlings were located during the searches in Sussex, but fewer than 30% in Essex. Our calculation of Jolly-Seber estimates of resighting and survival rates are compromised because very few birds are seen in Essex after day 14, however preliminary results indicate that estimated survivorship to 14 days is over 65% in Sussex but below 50% in Essex.

Further evidence of poor survivorship in Essex is that recruitment into the breeding population is markedly different between the two sites: over 50 adults colour-ringed as pulli were recorded breeding at the Sussex site in 1998; in Essex no pulli are known to have returned as breeding adults.

DISCUSSION

This overview illustrates how the analysis of extensive long-term BTO data and the execution of intensive field studies can be used to pursue an understanding of the demographic processes driving a long-term population decline. There remain many questions to be answered, but current results suggest that further effort should be focused on the environmental factors influencing first-year survival, particularly post-fledging survival, and the number of breeding attempts made by individual birds each season. Although the specific environmental processes responsible are not yet known, many hypotheses can now be ruled out, leaving only those that involve effects on these particular stages of the life cycle. Much work has already been devoted to the effects of predation (Thomson *et al*. 1998) and weather (Baillie 1990, Thomson *et al*. 1997), but there is no strong evidence that either is responsible for the Song Thrush population decline.

The extensive BTO monitoring programmes have not so far been used to estimate the number of breeding attempts. The Nest Record Scheme generally follows only the performance of individual breeding attempts. Further work may look for ways of estimating the number of breeding attempts indirectly from ringing data; these provide a measure of the ratio of young to adult birds in the population throughout the breeding season. From this measure of overall productivity, the number of breeding attempts can be calculated if clutch size, hatching success and fledging success can be calculated from the Nest Record data.

With fieldwork, we are currently looking at the environmental factors affecting both the number of breeding attempts and post-fledging survival. We are using intensive searches for colour-ringed Song Thrush fledglings 7 and 14 days after leaving the nest so as to measure the rate of post-fledging survival prior to dispersal and thus gain insights into the environmental processes that influence it. Post-fledging survival beyond this time is difficult to study with mark-resighting techniques at individual field sites because young birds disperse.

Given the magnitude of differences in demographic rates between sites, it would also seem wise to consider in more detail the role that changing frequencies of different habitats play in driving changes in the average rates nationally. In particular, if the population consists of a series of source and sink habitats then a slight change in the ratio of these could give rise to marked changes in national population size. Thus, for example, if wooded areas are productive sources and intensively farmed areas are strong sinks, then declines in the farmland populations could be more linked to changes in the wooded areas than to changes in the farmland itself.

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