

Using a State-Space Model of the British Song Thrush *Turdus philomelos* Population to Diagnose the Causes of a Population Decline

Stephen R. Baillie, Stephen P. Brooks, Ruth King, and Len Thomas

Abstract We investigated the utility of state-space models for determining the demographic causes of population declines, using the Song Thrush as an example. A series of integrated state-space models were fitted to census and ring-recovery data from the United Kingdom for the period 1968–2000. The models were fitted using Bayesian MCMC techniques with uniform priors and were ranked using the Deviance Information Criterion (DIC). Ring-reporting rates were modelled as a declining logit-linear function of year, with separate slopes for first-year birds and adults. The system process involved three demographic parameters, first-year survival, adult survival and productivity. Survival rates were modelled as year-specific, as specific to blocks with uniform population growth rates, or as logit-linear functions of weather or year. Productivity rates were modelled as random annual effects, as block-specific or as log-linear functions of year. We fitted 17 such models chosen on the basis of our prior knowledge of this system, given that it was not practical to fit all potential models. Six models within 10 points of the smallest DIC value were selected for inference. The posterior distributions from these preferred models suggest that population growth rates are best correlated with first year survival and that and that there is also a pattern of consistent but weaker correlations between population growth rate and adult survival. Correlations between population growth rates and productivity were more variable, and may have been influenced by errors in other parts of the model, as productivity is essentially measured by difference. Thus in this analysis the evidence for productivity having a substantial influence of population changes is equivocal. The interpretation of these results and the potential value of integrated state-space models for research into the population dynamics of declining populations are discussed.

1 Introduction

Many wild bird populations have declined in recent years as a result of large-scale environmental changes (Baillie et al. 2006). Some populations need to be managed

S.R. Baillie (✉)

British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK
e-mail: stephen.baillie@bto.org

D.L. Thomson et al. (eds.), *Modeling Demographic Processes in Marked Populations*,
Environmental and Ecological Statistics 3, DOI 10.1007/978-0-387-78151-8_23,
© Springer Science+Business Media, LLC 2009

541

to reduce their economic impacts or to protect other wildlife, while others need to be managed in ways that will produce a sustainable harvest. To address any of these management objectives it is important to understand the demographic and ecological processes that bring about population changes (Baillie 2001; Caughley 1994; Green 1995, 1999).

The British Trust for Ornithology operates an Integrated Population Monitoring programme, which monitors the abundance and demographic rates of a large number of widespread bird species (Baillie 1990). To-date most applied analyses of these data have involved estimating relative abundance and individual demographic rates from appropriate statistical models, and then exploring the consequences of these estimates using simple demographic models (Baillie and Peach 1992; Siriwardena et al. 1999; Thomson et al. 1997; Freeman and Crick 2003). Freeman et al. (2007) present a partially integrated approach where a population model is fitted directly to the site-specific census data but productivity and survival are still incorporated as “known constants” derived from separate statistical models. Fully integrated approaches allow parameter estimation and demographic modelling to be combined within a state-space model (Besbeas et al. 2002; Buckland et al. 2004; Thomas et al. 2005; Morgan 2008). Lapwing (*Vanellus vanellus*) data from the UK have been used to explore the use of this approach for birds. Models can be fitted using the Kalman filter under certain normality assumptions (Besbeas et al. 2002, 2005; Besbeas and Freeman 2006) or within a more general Bayesian framework based on MCMC methods (Brooks et al 2004; King et al. 2006).

Here we explore the use of state-space models to investigate the demographic causes of population declines using the Song Thrush (*Turdus philomelos*) population of the United Kingdom as an example. Unlike the Lapwing, for which the recovery analysis must be based on birds ringed as nestlings, we were able to model recoveries of Song Thrushes ringed as juveniles and adults. The population of this species declined by 51% between 1967 and 2003 (Baillie et al. 2006) and it is currently red listed. However, Song Thrushes are reasonably abundant and widely distributed in the UK, with an estimated population size of 1.1 million pairs (Gibbons et al. 1993; Baker et al. 2006). They have therefore continued to be reasonably well represented in demographic monitoring schemes throughout the period of the decline. The demographic causes of the decline of this species have been the subject of several previous studies (Baillie 1990; Thomson et al. 1997; Robinson et al. 2004). This earlier work provides a good basis for evaluating the potential role of state-space modelling.

2 Methods

2.1 *Field Methods and Sources of Data*

This analysis is based on a long-term series population data for Song Thrushes from Britain. Relative abundance was measured using territory counts from the Common

Birds Census and survival estimates were derived from ring recovery data. The data set analysed here was exactly the same as that used by Robinson et al. (2004) except that we have omitted recoveries of birds ringed as nestlings. Details of the data gathering methods have therefore not been repeated here. Methods of analysis are set out below.

2.2 Census Data

The census data were taken from the Common Birds Census using the years 1968–2000. This provides counts of the number of territories present on each plot in each year that it was censused, based on the mapping method. Many plot years are missing from the data set, due mainly to turnover of plots within the scheme. A population index and its variance were calculated using the method of King et al. (2006, Appendix A). Annual indices were calculated initially using a log-linear Poisson regression model fitted as a generalized linear model (GLM) with categorical site and year effects. Thus:

$$e_t = \left(\sum_{k=1}^K \exp(\alpha_k + \beta_t) \right)$$

where e_t is the index in year t , α_k is the site effect for year k and β_t is the year effect for year t , both from the GLM. The GLM also gives asymptotic standard errors for the site effects (s_k) and year effects (τ_t).

We used an estimate of the natural logarithm of the total number of territories present on all plots that had been included in the CBC during the study period (1968–2000) as an index of population size. We take logs here due to the skewness of the underlying distribution. Our new index was calculated by Monte Carlo integration using:

$$\gamma_t = \ln \left(\sum_{k=1}^K \exp(a_k + b_t) \right)$$

where γ_t is the index of abundance in year t , a_k is the site effect for year k and b_t is the year effect for year t . We treat a_k and b_t as random variables where:

$$a_k \sim N(\alpha_k, s_k^2) \text{ and } b_t \sim N(\beta_t, \tau_t^2)$$

and the two distributions are assumed independent. The γ_t are then calculated by drawing values of a_k and b_t from their respective distributions to obtain a series of values for γ_t and the sample mean taken as an estimate of the population index. Similarly the variance of the γ_t provides an estimate of the variance of the population index. This procedure gives an index on a log-normal scale, with variances that take full account of the errors in the site and year effects.

The census data were also used to identify periods with similar population growth rates (Fewster et al. 2000; Robinson et al. 2004). A generalized additive model with site effects and a smoothed trend function was fitted to the data. Significant turning points ($p < 0.05$) were identified from the second derivatives of the smoothed population trend by bootstrapping on sites. We based our analysis on logarithms of the smoothed series so that turning points would represent changes in the relative rate of population change. Within the time series from 1968 to 2000 turning points were identified in 1975, 1979, 1983, 1987, 1992 and 1998. These turning points were used to define blocks of years within which particular demographic parameters were assumed to be constant within some of our models (Table 1).

2.3 Ring Recoveries

The ring recovery models were based on a two age-class model where birds were ringed as juveniles and adults (Brownie et al. 1985). The analysis uses recoveries of Song Thrushes ringed as adults or as free flying juveniles between April and September. Details of exactly how recovery years were defined are given in Fig. 1 of Robinson et al. (2004). The numbers ringed in the first cohort and the expected frequencies of recoveries of birds ringed as adults (first row) and as juveniles (second row) in the first year of ringing and the first three years of recoveries are as follows:

$$\begin{array}{l} N_{a1} \quad N_{a1}(1 - S_{a1})\lambda_{a1} \quad N_{a1}S_{a1}(1 - S_{a2})\lambda_{a2} \quad N_{a1}S_{a1}S_{a2}(1 - S_{a3})\lambda_{a3} \\ N_{f1} \quad N_{f1}(1 - S_{f1})\lambda_{f1} \quad , \quad N_{f1}S_{f1}(1 - S_{a2})\lambda_{a2} \quad N_{f1}S_{f1}S_{a2}(1 - S_{a3})\lambda_{a3} \end{array}$$

Table 1 Seventeen combined models ranked using the deviance information criterion. The terminology used to define these models is given in the text

Model	First-year survival	Adult survival	Productivity	Number of parameters	Δ DIC
AWR	Year-specific	Drought	Random effects	73	0.0
BWR	Blocks	Drought	Random effects	48	0.1
AWB	Year-specific	Drought	Blocks	78	1.5
WWR	Frost	Drought	Random effects	43	3.2
AWY	Year-specific	Drought	Year trend	73	5.1
BWB	Blocks	Drought	Blocks	53	7.2
BAR	Blocks	Year-specific	Random effects	78	11.8
AAR	Year-specific	Year-specific	Random effects	103	13.2
BBR	Blocks	Blocks	Random effects	53	15.4
ABR	Year-specific	Blocks	Random effects	78	15.5
WAR	Frost	Year-specific	Random effects	73	16.2
WBR	Frost	Blocks	Random effects	48	17.9
AAV	Year-specific	Year-specific	Year trend	103	23.1
AAB	Year-specific	Year-specific	Blocks	108	24.0
BBB	Blocks	Blocks	Blocks	58	24.2
WAY	Frost	Year-specific	Year trend	73	38.3
YWB	Year trend	Drought	Blocks	48	44.5

The above example shows the full model where adult survival (S_a), first year survival (S_f), adult reporting rate (λ_a) and first year reporting rate (λ_f) all have annual parameters. N_{a1} represents the number of adults ringed in year 1 and N_{f1} the number of juveniles ringed in year 1. In all of our analyses we used reduced parameter models for some or all of these parameters as detailed below.

2.4 Modelling Ring Reporting Rates

A large number of ring reporting rate models for this data set were examined by Robinson et al. (2004). This included a model in which reporting rates were both age and year-specific, and various simpler models with additive age effects and with either year-specific or logit-linear effects of time. There was a significant decline in reporting rates with time, a pattern that has been found in several other datasets (Baillie and Green 1987; Freeman et al. 2007). There was strong support for a model that showed a logit-linear decline in reporting rate, with separate slopes and intercepts for the first year and adult age classes. This model was the most strongly supported for all nine parameterizations of survival rate considered by Robinson et al. (2004). Thus:

$$\text{logit}(\lambda_f) = a_f \text{ year} + b_f$$

$$\text{logit}(\lambda_a) = a_a \text{ year} + b_a$$

This model for reporting rates has therefore been used for all of the analyses presented in this paper.

2.5 Modelling Survival

The survival rates of Song Thrushes have been shown to be dependent on weather during both winter and summer (Thomson et al. 1997; Robinson et al. 2004). Their main food is soil invertebrates, particularly earthworms, which may become inaccessible during periods of severe winter weather. Similarly, drought may severely restrict access to soil invertebrates during the summer.

We extracted weather data for three weather stations that are broadly representative of Lowland England where most Song Thrushes are ringed. For each station we calculated the length of the longest consecutive period of freezing weather (mean air temperature < 0) between October and March and the length of the longest period of consecutive days with negligible rainfall (total daily rainfall less than 1 mm) between June and mid-August. These values were then averaged across the three weather stations and are referred to as frost days and drought days respectively (Robinson et al. 2004).

We therefore considered models where survival is a logit-linear function of weather. These were:

$$\text{logit}(S_f) = a_f \text{ frost} + b_f$$

$$\text{logit}(S_a) = a_a \text{ drought} + b_a$$

We restrict our modelling of relationships between weather and survival to these two equations following the earlier analysis of these data by Robinson et al. (2004). They found that modelling either first year or adult survival in relation to both frost and drought did not increase the amount of variation explained significantly. We also considered models in which survival was year-specific, block-specific or a logit-linear function of time. Block models assumed that survival rates of the age class concerned (first year or adult) were constant within periods of similar population growth rates, determined from turning points in the abundance trajectory as described above.

2.6 Modelling Productivity

Our data set did not include any explicit estimates of reproductive rates. Productivity was therefore calculated by difference using the overall measures of population change and the first year and adult survival data. The productivity measure used here therefore represents the number of young produced per breeding female up to the mean date when birds are ringed as juveniles. It therefore incorporates variation due to number of breeding attempts, number of fledglings produced per attempt and survival over the first 63 days after fledging (Robinson et al. 2004).

We initially considered a model with year-specific estimates of productivity. However, such a model is likely to result in over fitting where productivity is calculated by difference, because the estimated population growth rates from the demographic parameters will always be identical to those derived directly from the census data. We therefore fitted the following random effects productivity model:

$$P_t \sim N(P, \sigma^2)$$

where P_t represents the annual productivity effects, P is the mean productivity and σ^2 is the variance of the annual effects. This was incorporated in our integrated model as a Bayesian hierarchical model. P was assigned a normal prior with mean 1.0 and variance 10. σ^2 was assigned an inverse Gamma prior with parameters 0.001 and 0.001. We undertook additional simulations to check that our results were not sensitive to the exact priors chosen. Productivity was also modelled as, as constant within blocks of uniform population growth rates (block-specific) or as a log-linear function of year.

2.7 State-Space Model

To model the overall dynamics of the population we use a state-space model (Buckland et al. 2004) that comprises observation and system process components. The observation process involves a model of the annual CBC indices and their variances (but not their co-variances) derived using the method described above. We assume that the log of the population index is Normally distributed about the log of the true population size. Thus:

$$\ln y_t \sim N(\ln N_t, \sigma_t^2)$$

where y_t represents the observed annual population indices, N_t represents the true underlying numbers of females in the breeding population and σ_t^2 represents the year-specific variances of population size.

The system process is based on a simple Leslie matrix model. Song Thrushes breed when they are one year old. Survival rates of first year birds differ from those of older individuals but otherwise survival is assumed to be independent of age. Following earlier integrated models of the dynamics of bird populations (Besbeas et al. 2002; Brooks et al. 2004; King et al. 2006) we use a Poisson model to describe the number of offspring produced each year and a Binomial model to describe survival from one year to the next. Our model for the number of females in the population is based on the deterministic relationship:

$$N_t = N_{t-1}P_{t-1}S_{f,t-1} + N_{t-1}S_{a,t-1}$$

Thus we model the number of females in the population as:

$$N_t = N_{a,t} + N_{1,t}$$

where

$$N_{a,t} \sim \text{Bin}(N_{t-1}, S_{a,t-1})$$

and

$$N_{1,t} \sim \text{Po}(N_{t-1}P_{t-1}S_{f,t-1})$$

2.8 Fitting the Joint Model

In the state-space model we consider the population indices y as a function of true population size, productivity, first year survival, adult survival and the variances of the population indices. Thus we have:

$$f(y|N, P, S_f, S_a, \sigma_t^2) = f(y|N, \sigma_t^2) f(N|P, S_f, S_a)$$

where $f(y|N, \sigma_t^2)$ is the density corresponding to the observation process and $f(N|P, S_f, S_a)$ is the density corresponding to the system process.

The recovery data m are modelled as the product of multinomial distributions with parameters first year reporting rate, adult reporting rate, first year survival and adult survival. Thus we have:

$$f(m | \lambda_f, \lambda_a, S_f, S_a)$$

Under the assumption of independence between the census and recovery data we can obtain a joint probability distribution for the combined data as follows:

$$\begin{aligned} f(y, m | N, P, S_f, S_a, \sigma_t^2, \lambda_f, \lambda_a) \\ = f(y|N, P, S_f, S_a, \sigma_t^2) f(m | \lambda_f, \lambda_a, S_f, S_a) \end{aligned}$$

The models were fitted using Bayesian methods. We define priors on the parameters and then draw samples from the joint posterior distribution using MCMC methods.

The models were fitted using a purpose written FORTRAN program to perform sequential Metropolis-Hastings updates on each parameter in turn. We performed 1,000,000 iterations for each set of simulations and discarded the first 100,000 as burn in. The results were thinned by a factor of 10. Our various models took between 2 hours 24 min and 18 hours 42 min to run on various PCs (typically 2.8 GHz processors) running under Fedora Linux. Good convergence was achieved and model runs with different starting values gave similar results.

We did not have prior information that was independent of this study. Therefore survival rates were assigned uniform priors between 0 and 1.0 while productivity rates were assigned uniform priors between 0 and 2.0. Priors for regression coefficients and intercepts were normally distributed with means of 0 and variances of 100. The system equation for the state-space model is recursive, requiring the provision of a starting value for population size (N). The population index for this starting year (1968 in the present analysis) was treated as a normal prior with mean and variance obtained from the analysis of index values described above. Previous studies using similar state space models have found that the results are not sensitive to the exact choice of prior starting value (Brooks et al. 2004; King et al. 2006). This is to be expected, as this is effectively a model of relative abundance.

2.9 Model Selection

Our models included three demographic parameters (productivity, first year survival and adult survival) each of which could vary in four different ways (log or logit-linear function of weather, year-specific/random annual effects, block-specific or log or logit-linear function of time). This gave a set of 64 potential models. It was

not possible to fit all of these models using the MCMC methods described above due to constraints of computer time. We therefore selected 17 models that we felt were most likely to describe this system, based on previous work (Table 1). The fit of these models was compared using the Deviance Information Criterion (DIC). Differences in DIC values of more than 10 should definitely rule out the model with the higher DIC value, while differences between 5 and 10 may be regarded as substantial (Spiegelhalter et al. 2002).

2.10 Classical Analysis

We compare some of our results with those from a classical analysis of the same data set which did not incorporate any formal joint modelling of the census and recovery data. For these analyses standard recovery models were fitted using program MARK (White and Burnham 1999). Productivity was calculated as that required to give the observed population change given the survival estimates obtained from the MARK analyses.

3 Results

The new population index generated by simulation is very similar to the original index (Fig. 1). The small but systematic difference between the two indices is because the original index values represent the mode of a skewed distribution while the new index values represent the mean (King et al. 2006, Appendix A). The population declined from the start of the time series in 1968 until 1987, with the steepest decline from 1975 onwards. There were marked fluctuations in abundance between 1987 and 2000 but there was no clear long-term trend during this period.

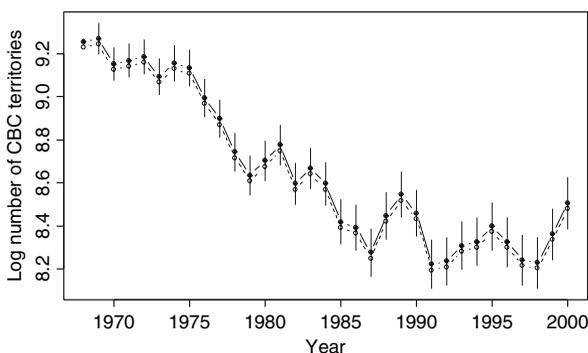


Fig. 1 Abundance of Song Thrushes on CBC plots between 1968 and 2000 calculated from the site and year effects by simulation (*filled circles* joined by *solid line*). Error bars are 95 percentiles from the simulation results. The open circles joined by a broken line show an index based only on the year effects from the generalized linear model. For further details of methods see text

Our integrated models aim to determine the demographic processes that brought about this pattern of population changes.

The numbers of parameters and delta DIC values for our 17 models are shown in Table 1. Six models had Δ DIC values of less than 10, including four with Δ DIC values of less than 5. In all six models adult survival was a logit-linear function of drought. First year survival was year-specific in three models, block-specific in two models and a function of frost on one model. Productivity had random annual effects in three models, block-specific effects in two models and showed a log-linear trend with year in one model. Thus there is good evidence of some form of year-specific variation for both first-year survival and productivity, while variation in adult survival appears to be well modelled as a function of drought. The only difference between the two best models (Δ DIC 0.1) is that one has fully year-specific first year survival, while the other has block-specific first year survival.

Ring reporting rates of both first year birds and adults showed a logit-linear decline with time. The details given here are based on model AWR (posterior means with 95% HPDIs for regression parameters: first year slope -0.424 , -0.566 to -0.282 ; first year intercept -3.616 , -3.782 to -3.437 ; adult slope -0.579 , -0.657 to -0.504 ; adult intercept -3.748 , -3.828 to -3.664) but results from the other five preferred models were similar. Reporting rates of first year birds were slightly higher than those of adults (Fig. 2a), a feature found in all six models. First year reporting rates from the MARK analysis were slightly higher than those from the integrated analysis in this model (Fig. 2b) but the differences were less than this in the other five models. In all six analyses the adult reporting rate estimates from MARK and from our integrated analysis were almost identical. Results from the best model (AWR) are plotted in Fig. 3. Broken lines show results from a similar model based on a conventional analysis, where N is taken from the CBC index, survival rates are modelled using Mark with the same parameterization as in model AWR, and annual productivity is calculated by difference. In model AWR the estimates of true population size from the state-space model closely match the original CBC index (Fig. 3a). The system error in the model is represented by a Poisson process and the pattern of system errors therefore closely follows that of true population size (Fig. 3b). Population growth rates from the integrated and classical analyses are similar (Fig. 3c) but the differences between the two approaches can be seen more clearly than in Fig. 3a.

Annual estimates of productivity (Fig. 3d) and first year survival (Fig. 3e) from the integrated model have relatively poor precision, even though the productivity values are shrinkage estimates from a random effects model. Nevertheless there is reasonably good agreement between the integrated analysis and the classical analysis in both cases. The poor precision of the first-year survival estimates was found in both the integrated and MARK analyses, and is likely to be a function of the number of recoveries available for this species. The logit-linear relationship between adult survival and drought days was very similar in both the classical and integrated analyses (posterior means and HPDIs from integrated analysis: intercept 0.509 , 0.427 to 0.592 ; slope -0.135 , -0.191 to -0.076). As a result of this the patterns

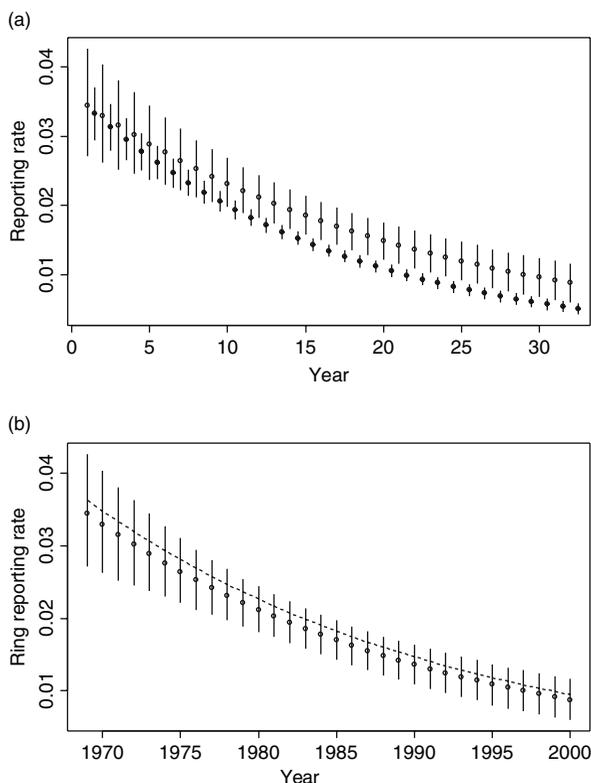


Fig. 2 Temporal trends in ring reporting rates of Song Thrushes, modelled as a logit-linear function of year. Error bars show 95% highest probability density intervals from MCMC analysis. (a) First year (*open circles*) and adult (*filled circles*) reporting rates from model AWR. (b) First-year reporting rates (*open circles with error bars*) from model AWR. Broken line shows the results of a stand-alone mark-recovery analysis of the same data conducted using program MARK

of annual variation in adult survival shown by the two analyses are almost identical (Fig. 3f).

The six best models (Table 2) all showed very similar patterns of change in the population index over time. Patterns of variation in population growth rates were very similar for the top five models ($r = 0.879\text{--}0.992$) but posterior mean population growth rates from model BWB showed a weaker relationship with those from the other models ($r = 0.749\text{--}0.823$). Posterior mean values for annual productivity were less strongly correlated between the different models. The three models that included random annual effects for productivity (AWR, BWR and WWR) showed moderate correlations between posterior mean productivity values ($r = 0.725\text{--}0.812$) as did the three models with block effects or a year trend (AWB, BWB and AWY, $r = 0.612\text{--}0.892$). Posterior mean first year survival rates were well correlated between the three models with year-specific first year survival (AWR, AWB and

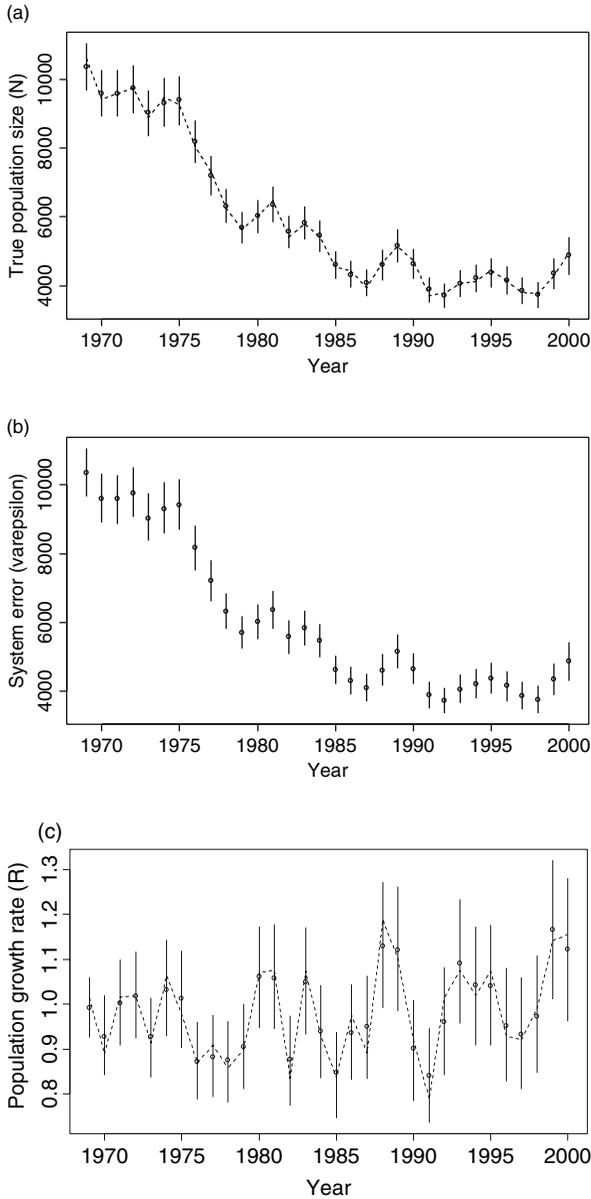


Fig. 3 Time-series of parameter estimates obtained by fitting joint model AWR with year-specific first year survival, adult survival modelled as a logit-linear function of drought days and productivity modelled as annual random effects (*open circles with error bars*). Values are posterior means with 95% highest probability density intervals. Results based on separate analyses of the census and ringing data are also shown (*broken lines*). For further details of methods see text. **(a)** Population size (N); **(b)** System error; **(c)** Population growth rate; **(d)** Productivity; **(e)** First-year survival; **(f)** Adult survival

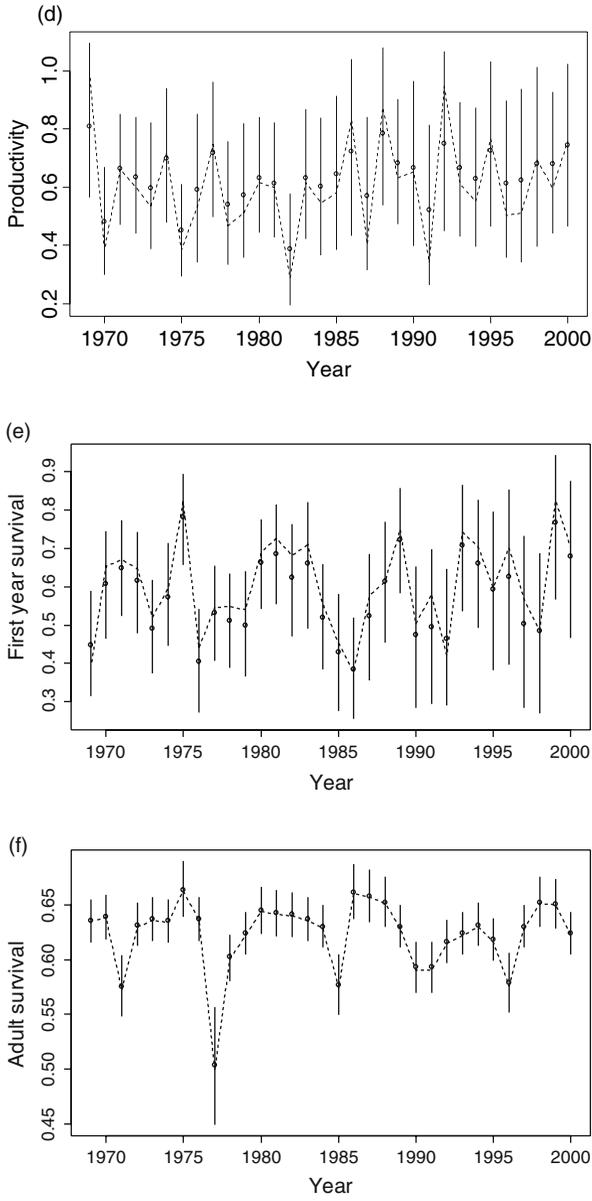


Fig. 3 (continued)

Table 2 Posterior means and 95 percentiles for correlations between population growth rate and demographic parameters. Results are presented for the six best model as ranked by DIC

Model	Δ DIC	Productivity			Correlation between growth rate and population First-year Survival					
		2.5 percentile	Mean	97.5 percentile	2.5 percentile	Mean	97.5 percentile	2.5 percentile	Mean	97.5 percentile
AWR	0.0	0.206	0.493	0.720	0.331	0.586	0.797	0.170	0.336	0.499
BWR	0.1	0.451	0.697	0.862	0.338	0.525	0.677	0.205	0.380	0.547
AWB	1.5	-0.053	0.323	0.607	0.406	0.725	0.900	0.296	0.437	0.571
WWR	3.2	0.583	0.798	0.926	0.405	0.550	0.678	0.200	0.385	0.559
AWY	5.1	-0.282	0.228	0.342	0.712	0.874	0.956	0.315	0.464	0.600
BWB	7.2	-0.506	0.114	0.660	-0.069	0.530	0.820	0.500	0.660	0.796

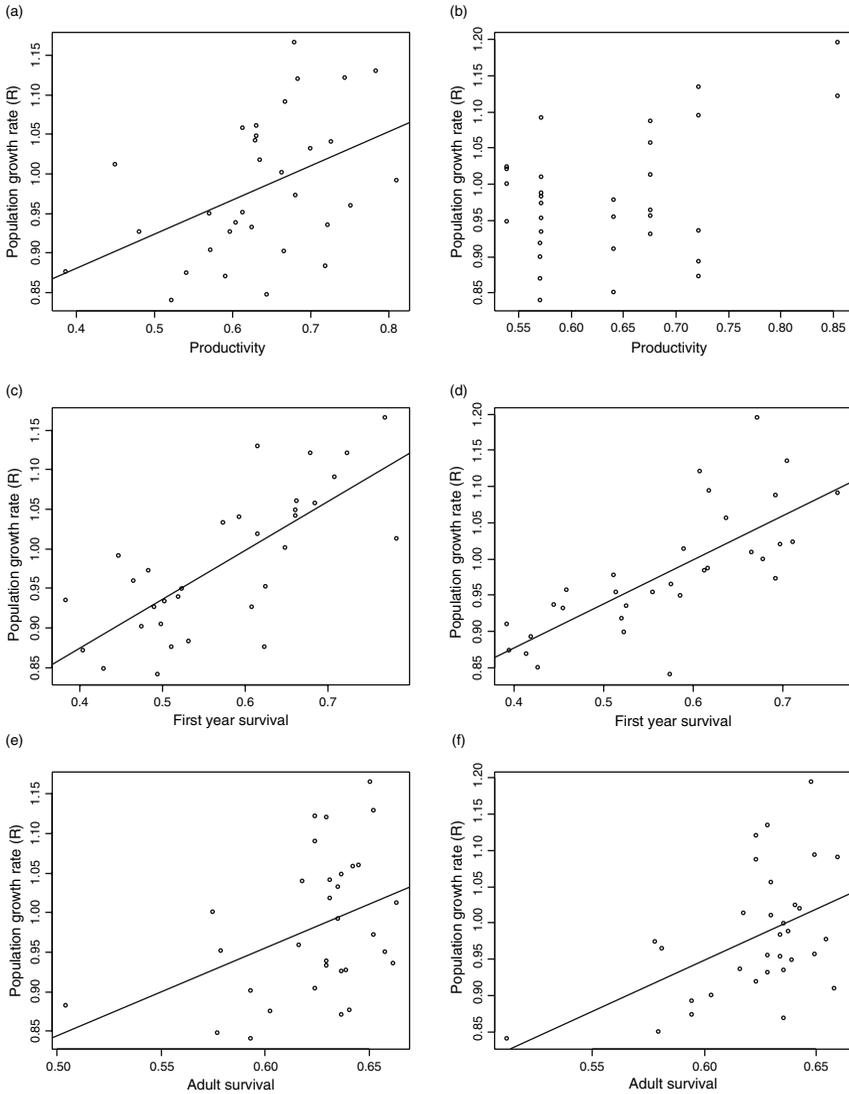


Fig. 4 Relationships between population growth rates and individual demographic parameters from two of our preferred models, AWR and AWB. Both models have year-specific first year survival rates and adult survival modelled as a logit-linear function of drought days. Productivity is modelled as either random annual effects (model AWR) or as constant within periods with uniform population growth rates (model AWB). Points are posterior means from the MCMC analysis. Lines show linear regressions where the 2.5 percentiles of the posterior correlation coefficients are greater than zero. **(a)** Productivity, model AWR; **(b)** Productivity, model AWB; **(c)** First-year survival, model AWR; **(d)** First-year survival model AWB; **(e)** Adult survival, model AWR; **(f)** Adult survival, model AWB

AWY, $r = 0.915\text{--}0.927$). Similarly the first year survival estimates between the two models with block-specific first year survival were well correlated (BWR vs BWB, $r = 0.949$). In contrast posterior mean first-year survival values from the model where first year survival was logit-linear function of frost days (WWR) were only moderately correlated with those from the other models ($r = 0.501\text{--}0.606$). The six best models all had adult survival modelled as a logit-linear function of drought, and posterior mean adult survival rates from all of these models were almost identical ($r > 0.999$ in all cases).

A key aim of this type of analysis is to quantify the contributions of changes in different demographic rates to overall population changes. To illustrate the patterns involved posterior means for annual population growth rates were plotted against posterior means for annual productivity, first year survival and adult survival. Sample plots for models AWR and AWB are presented in Fig. 4. The MCMC approach makes it straightforward to carry out formal tests of these relationships. Correlation coefficients for the above relationships were calculated separately using the results from each MCMC iteration. The distributions of these posterior correlation coefficients were then used to assess the strength of these relationships within each of our six preferred models (Table 2). Posterior mean correlations between population growth rate and productivity varied between 0.114 and 0.798, with the 2.5 percentile for three of the six models overlapping zero. In contrast posterior mean correlations between population growth rates and first year survival varied between 0.525 and 0.875, with only that from the model with the greatest delta DIC having a 2.5 percentile less than zero. Posterior mean correlations between population growth rate and adult survival were less than the equivalent correlations for first year survival in five out of six cases, and in all models the 2.5 percentile was greater than zero.

4 Discussion

4.1 *Demographic Causes of the Song Thrush Decline*

Analyses of the BTO's Song Thrush population data up to the 1980s indicated that there were no trends in nesting success or adult survival that could explain the decline (Baillie 1990). Indeed nesting success had actually increased, a pattern that has since been found in some other declining species and may be a density-dependent response to reduced abundance (Siriwardena et al. 2000). A subsequent analysis of first year and adult survival rates based on constant reporting rate models showed that the observed variation in first year survival was sufficient to explain the observed population decline (Thomson et al. 1997). Further more detailed analyses extended this work by including temporal variation in reporting rates and the estimation of post-fledging survival (Robinson et al. 2004). This block-specific analysis showed that population growth rates were well correlated with first year survival and more weakly correlated with post-fledging survival. There was no correlation with either productivity or adult survival.

The results from the present study are broadly consistent with these earlier analyses of this data set, with strong evidence that population growth rates are well correlated with first year survival. Adult survival is also correlated with population growth rates, although the correlation is weaker than for first year survival. Evidence for a correlation between productivity and population growth rate is equivocal, being sensitive to the choice of model within the set of models selected using DIC (Table 2). The three models where productivity is modelled using random annual effects all show a correlation between productivity and population growth rate but the other models do not. Productivity is essentially calculated by difference and it may therefore incorporate errors in the measurement of the other demographic parameters. Thus a correlation between population growth rate and productivity may partly reflect errors in other parameters or parameters that have not been measured adequately. While our use of a random effects model for productivity may have reduced problems of over-fitting, it will not solve this problem completely. Incorporation of direct measures of productivity from nest record cards or from juvenile to adult ratios in standardized catches could potentially improve the robustness of these results. It should be noted that our measure of productivity includes post-fledging survival (between ringing as a nestling and 63 days later), for which there is some previous evidence for a correlation with population growth rate. The addition of explicit estimates of post-fledging survival to our model would help to clarify this. This study suggests that all three demographic rates included in our model have some influence on population growth rates, as is to be expected. The main aim of such studies is to identify the relative contributions of these demographic parameters, as part of the process of constructing and testing hypotheses about the ecological causes of population changes.

To further explore the differences between the results of this study and those of Robinson et al. (2004) we examined the posterior correlations between population growth rates and demographic parameters using model BBB, with block-specific estimates similar to those from the earlier study. This model had poor support, being ranked 15 out of 17 on the basis of DIC (Table 1). Posterior mean correlation coefficients indicate that under this model population growth rate is most strongly correlated with first year survival ($r = 0.632$) and is only weakly associated with adult survival ($r = 0.227$) and productivity ($r = 0.127$), results that correspond well with the results from our preferred models, and also with those of Robinson et al. (2004). However, the HPDIs for all of these correlations substantially overlap zero.

The key environmental factors responsible for changes in the first year survival of Song Thrushes remain to be identified. Evidence for a range of candidate hypotheses that could explain this change has been reviewed elsewhere (Peach et al. 2004b; Robinson et al. 2004). Song Thrushes feed mainly on soil invertebrates, particularly earthworms, and reductions in the amount and quality of suitable feeding habitat are likely to have contributed to their decline. Important habitat changes are likely to include the loss of permanent pasture to arable and increased under-field drainage leading to more rapid drying out of the soil. There is also good evidence that Song Thrushes are affected by summer moisture levels in surface soils, which in

turn affect the availability of their earthworm prey (Peach et al. 2004a). Furthermore, Peach et al. (2004b) demonstrated a strong negative relationship between the percentage of land subjected to under-field drainage and regional changes in Song Thrush populations. This evidence fits well with the relationship between summer droughts and adult survival, which in turn influences population changes. Similar factors may also have affected first year survival, although there is no direct correlation between first year survival and summer drought.

Variation in summer food supply may also affect components of our productivity measure, particularly post-fledging survival. Intensive field studies have demonstrated that in a rapidly declining farmland population Song Thrushes were making too few nesting attempts to sustain the population (Peach et al. 2004b). However, these results are based on comparisons between two local populations after the main national decline had taken place. In contrast, national nest record card data show that success per attempt has increased over the period of the decline (Baillie 1990; Baillie et al. 2006). These two results are not necessarily contradictory but further work is needed to clarify the possible role of productivity changes in the decline of this species.

4.2 Utility and Development of Integrated Population Modelling

Integrated population modelling of the type presented here is a potentially powerful method for identifying the demographic mechanisms underlying population declines. The need to develop purpose written code currently restricts the speed with which these methods can be applied, and the ease of evaluating new models that may be proposed during the analysis. However, new general software for these types of methods is developing rapidly, and with increased computing power it should become much easier to perform such integrated analyses in the future. The code that we have developed for the analyses presented here will make it much easier to conduct similar analyses of other BTO population data.

We plan to extend the current study in a number of directions. Obvious first steps are to add explicit estimation of post-fledging survival to the model and to extend our use of random effects, particularly within the co-variate relationships (Hoyle et al. in prep.; Fonnesebeck et al. 2008). We also plan to incorporate more structural relationships within the models, particularly density-dependence (Lebreton 2008), through the use of a hierarchical modelling approach. Only being able to fit a small number of models was a limitation of the present study, although we did examine more models than in most other applications of these techniques to-date. The best way forward here is likely to be the application of reversible-jump MCMC to explore large model spaces. The use of this technique within an integrated population modelling framework has already been demonstrated by King et al. (2006). However, a substantial amount of development work will be needed to apply this technique to the range of models envisaged here. In the short-term one alternative approach may be to use techniques based on the Kalman Filter (Besbeas et al. 2002), which would allow certain classes of models to be fitted more rapidly. Another may be to apply the approach used by Maunder

(2004) for analyses of fisheries data. He developed models that use random effects (or approximations using penalized likelihood) rather than the state space framework (although these are arguably the same) because population sizes were very large and demographic uncertainty was minor.

In addition to ringing and census data the BTO operates a Nest Record Scheme that provides detailed data on individual nesting attempts (Crick et al. 2003). The statistical models used to estimate various components of nesting success can potentially be incorporated in an integrated population model in a way that is analogous to the ring recovery analyses used in this paper (Besbeas unpublished). The analysis presented here is based on only summary statistics derived from the census data. In principle it is possible to fit an integrated population model to the full sites by years matrix from the census data, thus incorporating the full variance–covariance structure of these data within the analyses (Besbeas and Freeman 2006). We do not currently know how much useful information would be obtained by increasing the complexity of the modelling process in this way but it seems likely that this might differ between datasets. Maunder (2001) found that integrated fisheries models showed little difference in point estimates but considerable reductions in estimates of uncertainty. This is probably because the integrated approach takes the covariance among years into consideration. This could also be achieved if the covariance of the years from the census data were included using a multivariate normal likelihood (Besbeas et al. 2003). Finally there is the potential to extend these methods to different types of ornithological monitoring data, such as the Constant Effort Sites Scheme. This scheme provides data on relative abundance, juvenile to adult ratios and mark-recapture survival data all measured at the same sites. Work to develop integrated Bayesian population models for these types of data is currently in progress (Cave et al. 2008).

Acknowledgments This work was undertaken while Stephen Baillie was on sabbatical at the Universities of Cambridge and St Andrews. He is grateful for the Statistical Laboratory, University of Cambridge and the Centre for Ecological and Environmental Modelling, University of St Andrews, for the provision of facilities and to the BTO for supporting this work. Rob Robinson provided data and results from his earlier analyses of these data and Chiara Mazetta gave advice on the analysis of the CBC data. Steve Freeman, Rob Robinson, Takis Besbeas and Mark Maunder provided helpful comments on an earlier version of this manuscript. The Common Birds Census and the Ringing Scheme are undertaken through a partnership between the BTO and the Joint Nature Conservation Committee (on behalf of Natural England, Scottish Natural Heritage, the Countryside Council for Wales and the Department of the Environment for Northern Ireland). This work is only possible due to many thousands of hours of field-work by volunteer census workers and ringers. We are very grateful to all of the above for their help and support.

References

- Baillie SR (1990) Integrated population monitoring of breeding birds in Britain and Ireland. *Ibis* 132:151–166.
- Baillie SR (2001) The contribution of ringing to the conservation and management of bird populations: a review. *Ardea* 89 (special issue):167–184.

- Baillie SR, Green RE (1987) The importance of variation in recovery rates when estimating survival rates from ringing recoveries. In North PM (ed.), *Ringing Recovery Analytical Methods*. *Acta Ornithologica* 23:41–60.
- Baillie SR, Marchant JH, Crick HQP, Noble DG, Balmer DE, Coombes RH, Downie IS, Freeman SN, Joys AC, Leech DI, Raven MJ, Robinson RA, Thewlis RM (2006) *Breeding Birds in the Wider Countryside: their conservation status 2005*. BTO Research Report No. 435. BTO, Thetford. (<http://www.bto.org/birdtrends>)
- Baillie SR, Peach WJ (1992) Population limitation in Palaearctic-African migrant passerines. *Ibis* 134(Suppl. 1):120–132.
- Baker H, Stroud DA, Aebischer NJ, Cranswick PA, Gregory RD, McSorley CA, Noble DG, Rehfisch MM (2006) Population estimates of birds in Great Britain and the United Kingdom. *British Birds* 99:25–44.
- Besbeas P, Freeman SN (2006) Methods for joint inference from panel survey and demographic data. *Ecology* 87:1138–1145.
- Besbeas P, Freeman SN, Morgan BJT, Catchpole EA (2002) Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58:540–547.
- Besbeas P, Freeman SN, Morgan BJT (2005) The potential of integrated population modelling. *Australian and New Zealand Journal of Statistics* 47:35–48.
- Besbeas P, Lebreton J-D, Morgan BJT (2003) The efficient integration of abundance and demographic data. *Applied Statistics* 52:95–102.
- Brooks SP, King R, Morgan BJT (2004) A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* 27:515–529.
- Brownie C, Anderson DR, Burnham KP, Robson DS (1985) *Statistical inference from band recovery data – A handbook*, second edition. United States Department of the Interior Fish and Wildlife Service, Resource Publication 156, Washington, DC.
- Buckland ST, Newman KB, Thomas L, Kösters N (2004) State-space models for the dynamics of wild animal populations. *Ecological Modelling* 171:157–175.
- Caughley G (1994) Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- Cave VM, Freeman SN, Brooks SP, Balmer DE (2008) On adjusting for missing visits in the indexing of abundance from ‘Constant Effort’ ringing. In: Thomson DL, Cooch EG, Conroy MJ (eds.) *Modeling Demographic Processes in Marked Populations*. Environmental and Ecological Statistics, Springer, New York, 3:949–964
- Crick HQP, Baillie SR, Leech DI (2003) The UK Nest Record Scheme: its value for science and conservation. *Bird Study* 50:254–270.
- Fewster RM, Buckland ST, Siriwardena GM, Baillie SR, Wilson JD (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology* 81:1970–1984.
- Fonnesbeck CJ, Edwards HH, Reynolds III JE (2008) Hierarchical covariate models for detection and availability of Florida manatees at a warm water aggregation site. In: Thomson DL, Cooch EG, Conroy MJ (eds.) *Modeling Demographic Processes in Marked Populations*. Environmental and Ecological Statistics, Springer, New York, 3:563–578
- Freeman SN, Crick HQP (2003) The decline of the Spotted Flycatcher *Muscicapa striata* in the UK: an integrated population model. *Ibis* 145:400–412.
- Freeman SN, Robinson RA, Clark JA, Griffin BM, Adams SY (2007) Changing demography and population decline in the Common Starling *Sturnus vulgaris*: a multisite approach to integrated population monitoring. *Ibis* 149:587–596.
- Gibbons DW, Reid JB, Chapman RA (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. T & A D Poyser, London.
- Green RE (1995) Diagnosing causes of bird population declines. *Ibis* 137(Suppl.):S47–S55.
- Green RE (1999) Applications of large-scale studies of demographic rates to bird conservation. *Bird Study* 46(Suppl.):S279–S288.
- Hoyle SD, Maunder MN, Veran S, Lebreton J-D (in prep.) A Bayesian integrated population dynamics model to evaluate the impact of fisheries on black-footed albatross using all available information.

- King R, Brooks SP, Mazzetta C, Freeman SN (2006) Identifying and diagnosing population declines: a Bayesian assessment of Lapwings in the UK. Technical Report, University of St Andrews.
- Lebreton JD (2008) Assessing density-dependence: where are we left? In: Thomson DL, Cooch EG, Conroy MJ (eds.) Modeling Demographic Processes in Marked Populations. Environmental and Ecological Statistics, Springer, New York, 3:19–42
- Maunder MN (2001) A general framework for integrating the standardization of catch-per-unit-of-effort into stock assessment models. Canadian Journal of Fisheries and Aquatic Science 58:795–803.
- Maunder MN (2004) Population viability analysis, based on combining integrated, Bayesian, and hierarchical analyses. Acta Oecologica 26:85–94.
- Morgan BJT (2008) Completing the ecological jigsaw. In: Thomson DL, Cooch EG, Conroy MJ (eds.) Modeling Demographic Processes in Marked Populations. Environmental and Ecological Statistics, Springer, New York, 3:513–540
- Peach WJ, Denny M, Cotton PA, Hill IF, Guar D, Barritt D, Impey A, Mallord J (2004a) Habitat selection by song thrushes in stable and declining farmland populations. Journal of Applied Ecology 41:275–293.
- Peach WJ, Robinson RA, Murray KA (2004b) Demographic and environmental causes of the decline of rural song thrushes *Turdus philomelos* in lowland Britain. Ibis 146(Suppl. 2):50–59.
- Robinson RA, Green RE, Baillie SR, Peach WJ, Thomson DL (2004) Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. Journal of Animal Ecology 73:670–682.
- Siriwardena GM, Baillie SR, Wilson JD (1999) Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. Ibis 141:621–636.
- Siriwardena GM, Baillie SR, Crick HQP, Wilson JD (2000) The importance of variation in the nesting success of seed-eating birds in determining their population trends on farmland. Journal of Applied Ecology 37:128–148.
- Spiegelhalter DJ, Best NG, Carlin BP, Van der Linde A (2002) Bayesian measures of model complexity and fit (with discussion). Journal of the Royal Statistical Society, Series B 2002 64:583–616.
- Thomas L, Buckland ST, Newman KB, Harwood J (2005) A unified framework for modelling wildlife population dynamics. Australian and New Zealand Journal of Statistics 47:19–34.
- Thomson DL, Baillie SR, Peach WJ (1997) The demography and age-specific annual survival of song thrushes during periods of population stability and decline. Journal of Animal Ecology 66:414–424.
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.