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A HIERARCHICAL ANALYSIS OF POPULATION CHANGE WITH APPLICATION TO CERULEAN WARBLERS

WILLIAM A. LINK[1] AND JOHN R. SAUER

USGS Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, Maryland 20708-4017 USA

Abstract. Estimation of population change from count surveys is complicated by variation in quality of information among sample units, by the need for covariates to accommodate factors that influence detectability of animals, and by multiple geographic scales of interest. We present a hierarchical model for estimation of population change from the North American Breeding Bird Survey. Hierarchical models, in which population parameters at different geographic scales are viewed as random variables, provide a convenient framework for summary of population change among regions, accommodating regional variation in survey quality and a variety of distributional assumptions about observer effects and other nuisance parameters. Markov chain Monte Carlo methods provide a convenient means for fitting these models and also allow for construction of estimates of derived variables such as weighted regional trends and composite yearly population indices. We construct an overdispersed Poisson regression model for estimation of trend and year effects for Cerulean Warblers (*Dendroica cerulea*), accommodating nuisance covariates for observer and start-up effects, and estimating abundance- and area-weighted annual indices at regional and continent-wide geographic scales. A goodness-of-fit test is also presented for the model. Cerulean Warbers declined at a rate of 3.04% per year over the interval 1966–2000.

Key words: Cerulean Warblers; Dendroica cerulea; *hierarchical models; Markov chain Monte Carlo; North American Breeding Bird Survey; population change; trends.*

INTRODUCTION

Observation of population declines has been a primary motivation for conservation actions (Caughley 1994); information on population status and change is an essential component of adaptive management and a variety of ecological studies. Unfortunately, information on population status is limited for many animal populations, and much of the existing information is controversial because of limitations of the surveys used to monitor species across their ranges. Few surveys provide the geographic coverage needed for range-wide monitoring of any species. Those that do tend to be deficient with regard to two primary statistical design issues: estimation of detection rates of animals within sample units, and poorly defined or incomplete sample units. Surveys with these limitations are often called index surveys. The numerical summaries produced by such surveys are not estimates of population size; their usefulness for estimation of temporal or spatial variation in population size depends on the validity of assumptions that may not be testable.

The North American Breeding Bird Survey (BBS; Robbins et al. 1986) is an index survey used to estimate population change of migratory birds. Counts on the BBS are conducted once each year along permanently located roadside survey routes, which are regarded as the sample units. No attempt is made to estimate the detectability of birds during counts. No estimate of population size (or population change) from the BBS can be made unconditionally; instead, all estimates are model-based, requiring assumptions about consistency in indices over time and space (Edwards 1998, Link and Sauer 1998*a*). Estimation of population change from index surveys is greatly complicated by such design inadequacies.

In particular, complications arise in the summary of count data over time and space. Simple averages of counts are generally inappropriate summaries of abundance (James et al. 1990), as it is evident that indices can be influenced by observer (Sauer et al. 1994), environmental conditions (Robbins et al. 1986), and habitat features (Sauer et al. 1995). The BBS is also subject to regional differences in numbers of routes and in the consistency of data collection along routes, so that some areas have large amounts of data whereas other areas have very limited data.

To accommodate such complications, Geissler and Sauer (1990) suggested a ''route regression'' procedure to estimate change from repeated surveys such as the BBS. In their formulation, rates of population change are estimated on each route using linear regression on log counts, with modeled effects of covariates accommodating differences in detectability associated with observers. More recently, route-specific estimates of trend have been obtained using estimating-equations estimators derived for count data (Link and Sauer 1994), using LOESS (James et al. 1996) and using negative binomial models (Link and Sauer 1998*a*). One

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[1] E-mail: william_link@usgs.gov

way or another, the essence of the route regression procedure is the same: route-specific estimates of trend are combined via weighted averages to obtain estimates of change at larger geographic scales.

The weightings used in route regression were an important innovation for summarizing population change for aggregates of routes. Precision weights accommodate variation in the quality of information, diminishing the contributions of imprecise estimates. Local abundance weights scale the trends to represent numbers of birds per route, so that aggregates can be produced representing total population change rather than a simple and misleading average trend. (It is misleading to summarize an increase of 50% on a route with 100 birds and a decrease of 50% on a route with 10 birds by a mean trend of zero.) Finally, because the number of routes varies spatially, estimates of total population change at large geographic scales are area weighted.

The route regression procedure has been legitimately criticized as ad hoc for the manner in which the precision and abundance weightings are calculated (ter Braak et al. 1994). Empirical Bayes methods suggested by Link and Sauer (1998*a*) and Sauer and Link (1999) offer some improvement on the precision weightings, but rely on asymptotic approximations and retain the ad hoc abundance weights in summary analyses. In this paper, we present hierarchical models for count survey data; these provide a very natural basis for large-scale summaries.

Estimation of population change from count survey data can be carried out using a hierarchical model relating patterns in data to patterns in population parameters. Most familiar statistical models have random variables that depend on fixed parameters. In hierarchical models, the parameters are treated as random variables; the probability distribution of the parameters is governed by further parameters, sometimes referred to as hyperparameters. For count-based surveys, this structure allows us to model the influence of regions, observers, and other factors on the distributions of the parameters influencing counts, rather than on the counts themselves. This eliminates the need for ad hoc procedures for accommodating regional differences in precision of counts in summary analyses.

Hierarchical models are naturally handled using Bayesian methods, which treat all unobserved and unknown quantities as random variables. The Bayesian paradigm requires specification of the *sampling distribution* of the data conditional on the parameters (as in classical statistical analysis), and also the specification of *prior distributions* for parameters. All Bayesian inference is based on *posterior distributions*, that is, the distributions of the parameters conditional on the data. Calculation of posterior distributions involves integration of the product of the sampling distribution and the prior distributions. Objective Bayesian analyses are conducted using prior distributions that provide little or no information about the parameters of interest: the prior is chosen in such a way as to produce a posterior distribution very similar to the likelihood function. Analytical calculation of the posterior is a difficult process, and often impossible, for most problems of practical use.

Markov chain Monte Carlo methods (MCMC; Gilks et al. 1996) provide alternative means of conducting analyses of hierarchical stochastic models. MCMC methods use simulation to evaluate probability distributions, and are thus similar to ordinary Monte Carlo methods. That is, features of the probability distributions studied are approximated by corresponding features of random samples drawn from the distributions; the sample mean, variance, and percentiles approximate the true mean, variance, and percentiles. The distinction is that ordinary Monte Carlo methods are based on independent samples from the distributions of interest, whereas MCMC is based on correlated samples, first-order Markov chains. This correlation requires that MCMC simulations be based on larger samples to obtain levels of precision comparable to those obtained using ordinary Monte Carlo methods. However, MCMC sampling is usually much more easily implemented than ordinary Monte Carlo sampling, because the probability distribution to be sampled need only be specified up to a multiplicative constant. In practical terms, this means that MCMC evaluation of a posterior distribution can be carried out without performing the analytically intractable integrals required for full specification of the posterior distributions.

We describe a hierarchical model for regional analysis of population change from BBS data, and fit it to data using Markov chain Monte Carlo methods. As an application of the procedure, we analyze population change for Cerulean Warblers (*Dendroica cerulea*) from BBS data for the interval 1966–2000.

Methods

The North American Breeding Bird Survey

The BBS contains design elements common to a wide variety of multiple-scale surveys. The BBS covers the United States (excluding Hawaii) and Canada, with limited coverage in Mexico. It is composed of >4000 roadside survey routes, each of which is 39.43 km in length. Routes contain 50 evenly spaced sample points, at which a competent observer conducts a 3-min point count during which all birds seen and/or heard are recorded. The sum of the counts from the 50 points in a year's survey is used as an index to abundance along the route for that year. Counts are conducted once each year, the same routes are surveyed every year, and generally the same observer will survey a route for a series of years. Most, but not all, routes are surveyed every year; routes in remote areas tend to be less consistently surveyed. Analyses of BBS data are summarized for states/provinces and for physiographic strata (e.g., Robbins et al. 1986, Link and Sauer 1998*a*).

Hierarchical model for analysis of change over time from BBS data

Attributes to be estimated.—Analyses of BBS data produce estimates of trend (average rate of yearly population change, for specific time intervals) and year effects, which are annual departures from the prevailing pattern of population change. Pattern of change is generally displayed using annual indices, which are fitted patterns of population change (based on estimates of year effects and trends), scaled to an index of regional abundance.

Nuisance effects to be controlled for.—There is considerable variability in the skills of BBS observers. Evidence has been presented that there is a temporal component to this variability, that observers' counts are partially explained by the year in which their service to the BBS began; loosely speaking, that the pool of observers has improved. Failure to account for observer effects has been shown to introduce substantial bias in trend estimation (Sauer et al. 1994). Our model therefore includes random effects, ω, for observers.

It has also been suggested that observers in the BBS tend to have lower than expected counts in the first year they conduct a survey (Kendall et al. 1996). Thus, our model includes a novice observer effect, η.

BBS counts are overdispersed relative to the Poisson distribution commonly used for counts (Link and Sauer 1997); replicate counts by the same observer on the same route and in the same year would be more variable than as indicated by a Poisson model. Failure to account for overdispersion leads to overstatement of the precision with which parameters are estimated. We include random effects ε to accommodate extra-Poisson variation.

Model.—Our model describes counts $Y_{i,j,t}$ by an overdispersed Poisson regression. Indices i and t represent stratum and year, with index j referring to unique combinations of route and observer; a discussion of problems associated with distinguishing route and observer effects is reserved for the *Discussion*. The expected value of $Y_{i,j,t}$, given the values of stratum-specific intercept, slope, and year effects (S_i, β_i, and $\gamma_{i,t}$), observer/route effects (ω_j), and overdispersion effects ($\varepsilon_{i,j,t}$), is denoted by $\lambda_{i,j,t}$ and is modeled as satisfying

$$\log(\lambda_{i,j,t}) = S_i + \beta_t(t - t^*) + \omega_j + \eta\mathbf{I}(j, t) + \gamma_{i,t} + \varepsilon_{i,j,t}. \tag{1}$$

Here, t^* is a baseline year from which change is measured, and $\mathbf{I}(j, t)$ is an indicator (0–1 variable) for the event that the count was in the first year of service of an observer. The observer/route effects, year effects, and overdispersion effects are treated as mean zero normal random variables. The use of random effects to model weak stochastic relations among parameters is discussed in Link (1999).

Using classical (Frequentist) statistical descriptions, stratum and novice observer effects are ''fixed effects'' and all of the other effects in Eq. 1 are ''random effects.'' Under the Bayesian paradigm, a slightly different distinction is required, because *all* unknown quantities are treated as random variables. Instead of random and fixed effects, we distinguish *parameters* and *hyperparameters*: the prior distributions of parameters are governed by other parameters and hyperparameters, whereas the prior distributions of hyperparameters are completely specified. We used standard noninformative priors for the hyperparameters, as we will describe.

The hyperparameters S_i, β_i, and η are given diffuse (essentially flat) normal distributions. The default used in program BUGS (Spiegelhalter et al. 1995) specifies mean zero and standard deviation 1000, a density that varies by less than 0.005% on the range $(-10, 10)$, a range certain to include the true values of these effects.

Year effects, observer effects, and overdispersion effects were specified as having mean zero normal distributions. The observer effects were identically distributed, all having the same variance σ^2_ω. Similarly, the overdispersion effects were identically distributed with common variance σ^2_ε. The variance of the year effects was allowed to vary among strata; we denote these variances by $\sigma^2_{\gamma,i}$. These variances are hyperparameters, all with flat inverse gamma distributions. The default for such in BUGS has mean of 1 and variance of 1000; these are essentially equivalent to flat normal priors on the log of the precision.

It should be noted that species are not necessarily encountered on all routes in strata where they occur. We fit the model to data from routes on which a species was encountered by at least one observer, so that in order for S_i to reflect typical local abundance within the stratum (number of birds per route, e.g., Link and Sauer 1998*b*), it must be scaled by the proportion of routes on which the species was ever encountered, z_i.

Summaries.—Composite trends and composite annual indices are functions of the model's parameters and hyperparameters, combined using abundance weights reflecting the typical magnitude of counts on routes in the strata.

We define stratum-specific annual indices by

$$n_{i,t} = z_i \exp(S_i + \beta_i(t - t^*) + \gamma_{i,t}).$$

These indices reflect stratum-specific relative abundances of the species, adjusted for differences among observers; $n_{i,t}$ is an index to the number of birds per route in stratum i at year t. For comparisons among strata, we take n_{i,t^*}, the value for year t^*, as a baseline abundance for stratum i. Indices for stratum totals are obtained as $N_{i,t} = A_i n_{i,t}$, where A_i is the area of the stratum. Composite indices for collections of strata are sums of $N_{i,t}$'s.

Trend has been defined as an interval-specific geometric mean of proportional changes in population size (Link and Sauer 1998*a*), expressed as a percentage.

Thus the trend from year t_a to year t_b for stratum i is $100(B_i - 1)\%$, where

$$B_i = \left\{\frac{n_{i,t_b}}{n_{i,t_a}}\right\}^{1/(t_b - t_a)}.$$

If $N_t = \Sigma_i N_{i,t}$ is a composite index, the composite trend $\bar{B}$ is calculated analogously, as $100(\bar{B} - 1)\%$, where

$$\bar{B} = \left\{\frac{N_{t_b}}{N_{t_a}}\right\}^{1/(t_b - t_a)}.$$

Composite indices N_t represent total numbers of individuals; it is often useful to scale the index by the total area, obtaining a summary on the scale of birds per route, $n_t = N_t/\Sigma_i A_i$. This scaling may help to emphasize that the numbers reported are indices to abundance, rather than actual numbers of individuals. The value n_{t^*} provides a baseline abundance at the composite scale.

It should be noted that B_i, $\bar{B}$, $n_{i,t}$, and $N_{i,t}$ are *derived parameters*, that is, functions of the basic parameters describing the model, rather than basic parameters themselves. Their posterior distributions are easily evaluated using the Markov chains produced to study the parameters from which they are derived. The ease with which such summaries are evaluated in the context of hierarchical models, rather than through post hoc summarization of collections of parameter estimates, is a major advantage of Bayesian over classical methodology.

The graphical presentation of indices is of special importance for reporting analyses of count survey data. We recommend that graphical presentations of indices include posterior means (a Bayesian point estimate) and credible intervals (Bayesian confidence intervals, based on percentiles of posterior distributions). However, we note that plots of indices against time are often examined to illustrate temporal variability in population size. In Bayesian analyses, posterior means are optimal in the sense of minimizing quadratic loss in estimation of groups of related parameters; they are optimal estimates of *individual* values, in the context of the group. However, the *collection* of posterior means tends to be underdispersed relative to the collection of true parameters (Ghosh 1992). For the year effects, this means that the mean squared value of posterior means of $\gamma_{i,t}$ tends to be smaller than the variance of the normal distribution from which the individual values are sampled. Consequently, plots of indices against time may suggest greater stability than is appropriate; the posterior means are excessively smoothed. A simple expedient is to include plots of variance-inflated indices, calculated using adjusted year effects estimates $\hat{\gamma}_{i,t}^{\mathrm{CB}}$ instead of the posterior means of $\gamma_{i,t}$; the adjusted values are $\hat{\gamma}_{i,t}^{\mathrm{CB}} = \sqrt{C_i}\gamma_{i,t}$, where C_i is the ratio of the posterior mean variance for year effects in stratum i, $\sigma^2_{\gamma,i}$, to the mean squared value of posterior means of year effects. The superscript ''CB'' affixed to the adjusted year effects indicates that the adjusted estimate is a ''constrained Bayes'' estimate (sensu Ghosh [1992]; for an application of constrained Bayes estimation to count survey data, see Link and Sauer [1996]). Although the posterior means of annual indices remain the best mean squared error estimates of individual values, the variance-inflated values are useful for graphical displays, in that they more appropriately portray the magnitude of temporal variability in the indices.

Fitting the hierarchical model

We used program BUGS (Spiegelhalter et al. 1995) to fit the hierarchical model. BUGS is a convenient tool for formulating models and conducting MCMC analysis using Gibbs sampling and other procedures. Using MCMC results requires the Markov chain to have moved from initial values into a stationary distribution; in practice, this is provided for by discarding early observations of the chain (the ''burn-in''). We evaluated the convergence of the Markov chain to the posterior distribution using the Gelman-Rubin diagnostic, included with BUGS and described in its documentation (Spiegelhalter et al. 1995).

Example analysis: Cerulean Warblers

The Cerulean Warbler is a migratory species that breeds in a variety of forested habitats in eastern North America and winters primarily on the eastern slopes of the Andes in South America (see Plate 1). As a species that breeds high in forest canopies, it has been considered to be vulnerable to habitat changes in its breeding range. Several studies have documented declines based on BBS data (e.g., Robbins et al. 1992).

Although the BBS provides considerable data for the species, most information is based on relatively small counts on survey routes, raising concerns about the quality of the results. Here, we analyze Cerulean Warbler results from the BBS using the hierarchical model, and we compare results to those of the route regression procedure (Link and Sauer 1994).

Regions for analysis.—We use Bird Conservation Regions (BCRs) developed for the North American Bird Conservation Initiative, based on ecoregions described by the Commission for Environmental Cooperation (1997),[2] as the primary strata for analysis. Generally, BBS analyses have used physiographic regions within states/provinces as the strata for analyses (e.g., Geissler and Sauer 1990), but because Cerulean Warblers are encountered at low abundances over much of their range, we needed to aggregate BCR regions to obtain sufficient samples of routes for analysis, leading to these strata: (1) a Lower Great Lakes/St. Lawrence Plain stratum (BCR 13) that contained peripheral routes in Boreal Hardwood Transition and Atlantic Northern Forest strata, (2) Eastern Tallgrass Prairie (BCR 22),

[2] URL: ⟨http://www.bsc-eoc.org/international/bcrmain.html⟩

PLATE 1. Adult male Cerulean Warbler (at least 7 years old), photographied in eastern Ontario in 1997 by Jason Jones.

(3) Prairie Hardwood Transition (BCR 23), (4) Central Hardwoods (BCR 24), (5) a combined West Gulf Coastal Plain/Ouachitas (BCR 25) that contained a small part of the Mississippi Alluvial Valley stratum, and (6) a Piedmont stratum (BCR 29) that also contained portions of the Southeastern Coastal Plain and New England/mid-atlantic Coast strata. The Appalachian Mountains were divided into four strata: (7) Appalachian Mountains East (Maryland, Virginia, and North Carolina; BCR 28 East), (8) Appalachian Mountains West (Ohio, Kentucky, Tennessee, and Alabama; BCR 28 West), (9) Appalachian Mountains North (New Jersey, Pennsylvania, and New York; BCR 28 North), and (10) Appalachian Mountains–West Virginia (BCR 28 WVa).

Analysis.—For each region, we used the hierarchical model and program BUGS to estimate trend and annual indices. We used data from the entire BBS period of 1966–2000 and generated five independent Markov chains, each of length 25 000, of which we discarded the first 5000 values as a burn-in. These replicate chains were used for the Gelman-Rubin diagnostic (Spiegelhalter et al. 1995, Brooks and Gelman 1998), which compares within-chain and between-chain variability, and provided confirmation that the posterior distributions were adequately sampled by the MCMC algorithm. Our estimates of posterior distributions were based on the 100 000 ($= 5 \times 20\,000$) sampled values. We used $t^* = 1983$ as the ''fixed year'' for scaling results. For comparison with results of the hierarchical analysis, we also conducted a route regression analysis (Link and Sauer 1994, Geissler and Sauer 1990) of data using the composite regions.

We evaluated goodness of fit using a posterior predictive check based on the χ^2 discrepancy, as described by Gelman et al. (1995: Chapter 6). For each of the 100 000 sets of parameters sampled under the MCMC simulation, a replicate data set was generated according to the model specification. The value

$$T(\text{Data, Parameters}) = \sum_{i,j,t} \frac{(Y_{i,j,t} - \lambda_{i,j,t})^2}{\lambda_{i,j,t}}$$

was computed for the original data and each replicate data set. A Bayesian test of goodness of fit is based on the frequency with which T(Original Data, Parameters) exceeds T(Replicate Data, Parameters); this frequency is the Bayesian P value. For details, see Gelman et al. (1995: Chapter 6).

RESULTS

There were 8585 counts, produced by 1306 observers, on survey routes where at least one Cerulean Warbler was observed during the 1966–2000 interval: 75.9% of the counts are zeros, 12.2% are ones, and only 3.3% are ≥ 5.

Area weights and sample sizes vary greatly among the 10 strata (Table 1), as do the proportions of routes on which the species was encountered (z_i; Table 1). Values of z_i and baseline abundance n_{i,t^*} are low, reflecting the rarity of Cerulean Warblers.

The Bayesian goodness-of-fit test yielded a P value of 0.177; although this result cannot be interpreted as proof of the adequacy of the model (as is always the case with goodness-of-fit testing), it compares favorably with a similarly computed P value of 0.042 for the same model, but with overdispersion effects omitted.

The novice observer effect, η, was estimated as -0.029, with posterior standard deviation (i.e., standard error) of 0.059; our analysis thus provides little evidence of the postulated effect for counts of this species.

TABLE 1. Trend estimates by stratum for Cerulean Warblers in Bird Conservation Regions.

	Stratum descriptions			Hierarchical analysis			Route regression trend per yr (%)	Efficiency gain†† (%)
Bird conservation region	z†	R‡	Area§ (sq. miles)	Per yr‖ (%)	95% CI¶	n_{i,t^*}#		
Lower Great Lakes/St. Lawrence	0.12	(418)	761 863	0.50	(−2.32, 3.20)	0.0023	1.54	65
Eastern Tallgrass Prairie	0.15	(170)	321 560	−5.95	(−11.79, −0.51)	0.058	−9.52	31
Prairie Hardwood Transition	0.26	(127)	219 254	−4.23	(−7.33, −1.12)	0.32	−6.67	39
Central Hardwoods	0.49	(128)	302 897	−3.79	(−5.32, −2.26)	0.0020	−6.25	51
West Gulf Coastal Plain/Ouachitas	0.15	(66)	146 425	−13.86	(−20.49, −7.31)	0.0057	−14.99	21
Piedmont stratum	0.13	(277)	381 134	−0.52	(−8.03, 5.20)	0.016	−4.56	76
Appalachian Mountains East	0.46	(67)	65 586	−2.01	(−4.52, 0.30)	0.076	−1.76	−35
Appalachian Mountains West	0.58	(99)	140 132	−3.48	(−5.15, −1.85)	0.0061	−3.37	2
Appalachian Mountains North	0.47	(137)	138 480	−0.46	(−2.08, 1.10)	0.059	−1.44	21
Appalachian Mountains–West Virginia	0.85	(60)	62 911	−2.65	(−4.23, −0.91)	0.67	−3.24	−6
Species range	0.28	(1529)		−3.04	(−4.02, −2.07)	0.061	−3.29	30

† Proportion of Breeding Bird Survey routes on which the species was encountered.
‡ Number of routes in stratum.
§ Area of each stratum (1 square mile = 2.59 km^2).
‖ Trend estimate (percentage change per year, posterior mean).
¶ 95% credible intervals (2.5th and 97.5th percentiles of posterior distributions.
# Baseline abundance.
†† Estimated gain in efficiency associated with hierarchical analysis (1 − ratio of squared confidence interval length).

Estimates of population trend (Table 1) indicate that the population experienced substantial declines. Nine of the 10 composite strata had negative trend estimates, and the overall trend was −3.04% per year (Table 1). These results are similar to those produced by route regression; however, the efficiency of estimation (as measured by the ratio of squared confidence interval length) is typically greater using the more sophisticated and less ad hoc analytical methods.

The annual indices (Fig. 1) indicate substantial regional differences in patterns of population change. The composite indices (Fig. 2) reflect total population change, accounting for regional differences in trend, abundance, and stratum area. Constrained Bayes estimates in Figs. 1 and 2 provide a more realistic assessment of temporal variation in population size. We note that estimates based on the route regression procedure (Fig. 2) appear to be even less variable (i.e., oversmoothed) than the posterior means, although the overall pattern of decline is in evidence in either analysis.

DISCUSSION

There is a wide variety of methods for the analysis of count data such as those collected in the BBS. Various overdispersed generalized linear models have been applied to similar data sets (e.g., ter Braak et al. 1994, Link and Sauer 1998*a*), as have generalized additive models (James et al. 1996, Fewster et al. 2000). Generally, if these methods adequately incorporate the constraints imposed by the data collection and survey design, they provide similar results (Link and Sauer 1998*a*). However, accommodating the large differences in quality of information among regions has always made aggregation of results at regional scales problematic (e.g., Link and Sauer 1998*a*).

Hierarchical models provide a natural framework for estimation and regional summary of surveys such as the BBS. Our model accommodates regional differences in precision, with obvious consequences for estimation in areas with less information (Table 1). The MCMC procedure provides a convenient tool for estimation of composite results similar to those provided by route regression estimates. Unlike the route regression estimators, however, these estimators do not contain ad hoc weights; the weighting factors are part of the model. The hierarchical model presented here is the first alternative posed to the route regression method that contains the summary attributes needed to model regional population change.

As in all hierarchical analyses, the distributional assumptions placed on the parameters can influence the results. The smaller variances of the hierarchical model trend estimates are characteristic of the richer model structure used; parameter estimation is improved, conditional on the model, by consideration of individual parameters in the context of related parameters. Any analysis of regional population change of survey data such as the BBS places similar constraints on the analysis (e.g., through choice of weightings of trend estimates from more local geographic scales). Hierarchical modeling makes these assumptions explicit, and also allows their evaluation through alternative specifications of prior distributions.

Bayesian analysis also includes specification of probability distributions for hyperparameters. In our analysis, we used standard noninformative (''flat'') priors, reflecting the lack of prior information about hyperparameters (for a discussion, see Box and Tiao 1992). The choice of noninformative priors has received considerable attention in Bayesian literature, and criticism from one set of partisans in the historical Bayesian/Frequentist philosophical debate. The prob-

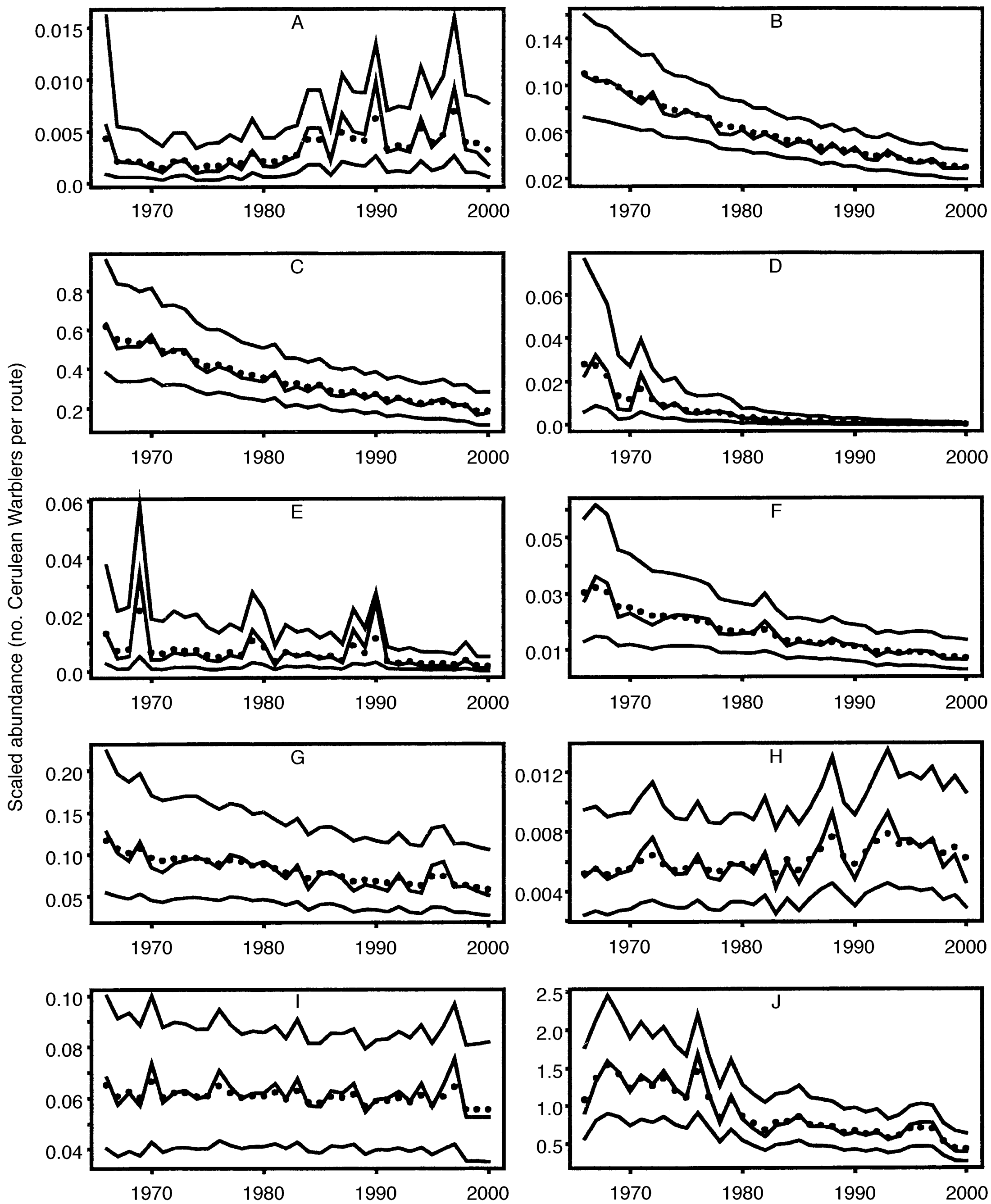

FIG. 1. Regional time series of annual indices $n_{i,t}$ for Cerulean Warblers (*Dendroica cerulea*) from hierarchical analysis of the North American Breeding Bird Survey. Strata are (A) Lower Great Lakes/St. Lawrence Plain (13), (B) Eastern Tallgrass Prairie (22), (C) Prairie Hardwood Transition (23), (D) Central Hardwoods (24), (E) West Gulf Coastal Plain/Ouachitas (25), (F) Piedmont stratum (29), (G) Appalachian Mountains East (28 East), (H) Appalachian Mountains West (28 West), (I) Appalachian Mountains North (28 North), and (J) Appalachian Mountains–West Virginia (28 WVA). Years are shown on x-axes; y-axes are abundances, scaled to no. birds/route. Solid circles are posterior means; the solid line nearly coincident with the circles indicates constrained Bayes estimates. Uppermost and lowermost solid lines in each panel provide 95% credible intervals for annual indices.

lem is essentially this: suppose that a model has a parameter θ, and that a flat prior is specified for θ. If the model were reparameterized using $\varphi = q(\theta)$, the resulting prior on φ would not be flat. Of course, a very similar problem exists when using a Frequentist analysis in choosing an unbiased estimator. Unbiasedness is not transformation invariant: the sample variance S^2 is unbiased for σ^2, but S is biased for σ. However, in

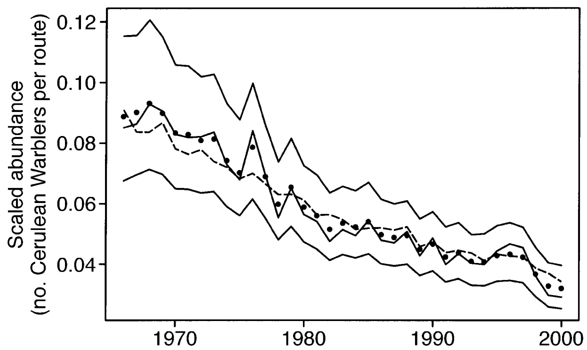

FIG. 2. Time series of annual indices n_t from the hierarchical analysis of Cerulean Warbler population change from the North American Breeding Bird Survey (solid circles), with associated 95% credible intervals. The solid line nearly coincident with the circles indicates constrained Bayes estimates. Years are shown on *x*-axes; *y*-axes are abundances, scaled to no. birds/route. For comparison, the dashed line indicates annual indices derived from the route regression analysis.

both cases, the putative problems are of little significance unless very small sample sizes are anticipated.

The model that we have presented here has at its heart a loglinear pattern of population change with identically distributed year effects accounting for departures from the underlying loglinear pattern. Alternative models might be considered with more or less underlying structure, all within the hierarchical framework described here. For example, one could choose a model in which yearly effects are modeled as fixed effects (hyperparameters, in the Bayesian development presented here) without any underlying loglinear pattern or association. This type of model has the advantage of flexibility for modeling abrupt changes in population size, such as have been documented for Carolina Wrens, *Thryothorus ludovicianus* (Link and Sauer 1998*a*), but it requires more and better data than for the model presented here. Our experience with BBS data indicates that fixed year effects models frequently cannot be fit at desired geographic scales. Another alternative is to treat year effects as a stationary autoregressive process (as in Breslow and Clayton 1993); this serves to smooth the year effects without specification of a particular pattern of population change. All of these alternatives fit neatly within the hierarchical modeling approach illustrated here. Migratory bird management and conservation uses of survey data most frequently need estimates of population change and annual indices of abundance; the definitions of trend and indices presented here are appropriate for any such formulation.

The model that we used has fixed effects for strata and random effects for combinations of route and observer. As a matter of interest, it would be desirable to distinguish random effects for routes within strata and for observers within routes. The limitations of BBS data, and specifically of those for low abundance and uncommon species such as the Cerulean Warbler, present problems for such modeling attempts. Because annual counts on routes are not performed by replicate observers, these route/observer effects are confounded; distinguishing them is, of necessity, a model-based exercise. Even in the context of a reasonable model, there are typically only 4–5 observers per route over the 35-yr period (Link and Sauer 1998*a*); there is little information for partitioning the variation. Also, evidence has been presented that the pool of observers is not temporally stationary; that new observers tend to count more birds than the observers they replace, even having controlled for changes in population size (Sauer et al. 1994, Link and Sauer 1998*b*); and for novice observer effects. Additional modeling of the observer/route effects could be conducted in the hierarchical framework presented here, subject to the limitations of the data. For instance, using the BBS Cerulean Warbler data, we modeled temporal changes in the pool of observers using the observer's first year of count on the route as a covariate governing the distribution of random effects for observer/route combinations. The resulting model showed the same pattern among observers as evidenced elsewhere (Link and Sauer 1998*b*), but introduced only minor changes to estimates of trend (a shift in estimates of composite trend by -0.4% per year), and hence is not reported here.

The BBS is not particularly well suited for monitoring Cerulean Warblers. Relatively few individuals of the species are encountered on survey routes over much of their range, because the roadside sample only covers a limited portion of the habitats favored by the species. The low abundances and limited access to Cerulean Warbler habitat have led to much speculation about whether the change in the segment of the population that is surveyed by the BBS is representative of change in the entire population. This deficiency of the survey could only be addressed by modifying the survey design to sample habitats away from roadsides. However, it is interesting to note that population estimates derived from BBS data tend to be larger than estimates based on Atlas data (Rosenberg et al. 2000), suggesting that roadside counts do not necessarily encounter fewer Cerulean Warblers than do observations not limited to roads.

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