

# An integrated population model for bird monitoring in North America

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**Abstract.** Integrated population models (IPMs) provide a unified framework for simultaneously analyzing data sets of different types to estimate vital rates, population size, and dynamics; assess contributions of demographic parameters to population changes; and assess population viability. Strengths of an IPM include the ability to estimate latent parameters and improve the precision of parameter estimates. We present a hierarchical IPM that combines two broad-scale avian monitoring data sets: count data from the North American Breeding Bird Survey (BBS) and capture–recapture data from the Monitoring Avian Productivity and Survivorship (MAPS) program. These data sets are characterized by large numbers of sample sites and observers, factors capable of inducing error in the sampling and observation processes. The IPM integrates the data sets by modeling the population abundance as a first-order autoregressive function of the previous year’s population abundance and vital rates. BBS counts were modeled as a log-linear function of the annual index of population abundance, observation effects (observer identity and first survey year), and overdispersion. Vital rates modeled included adult apparent survival, estimated from a transient Cormack-Jolly-Seber model using MAPS data, and recruitment (surviving hatched birds from the previous season + dispersing adults) estimated as a latent parameter. An assessment of the IPM demonstrated it could recover true parameter values from 200 simulated data sets. The IPM was applied to data sets (1992–2008) of two bird species, Gray Catbird (*Dumetella carolinensis*) and Wood Thrush (*Hylocichla mustelina*) in the New England/Mid-Atlantic coastal Bird Conservation Region of the United States. The Gray Catbird population was relatively stable (trend +0.4% per yr), while the Wood Thrush population nearly halved (trend –4.5% per yr) over the 17-yr study period. IPM estimates of population growth rates, adult survival, and detection and residency probabilities were similar and as precise as estimates from the stand-alone BBS and CJS models. A benefit of using the IPM was its ability to estimate the latent recruitment parameter. Annual growth rates for both species correlated more with recruitment than survival, and the relationship for Wood Thrush was stronger than for Gray Catbird. The IPM’s unified modeling framework facilitates integration of these important data sets.

**Key words:** avian demography; Bayesian hierarchical models; Breeding Bird Survey; MAPS program; population growth; U.S. Geological Survey; vital rates.

## INTRODUCTION

Integrated population models (IPMs) are a recent development in population ecology, providing a unified framework for analysis and inference from multiple population monitoring data sets (Besbeas et al. 2002, 2003, Abadi et al. 2010a, Schaub and Abadi 2011, Robinson et al. 2014). IPMs can be used to infer demographic parameters, assess population viability, and potentially improve the accuracy and precision of parameter estimates (Besbeas et al. 2005, Schaub and Abadi 2011, Hostetler et al. 2015, Lee et al. 2015). To date, IPMs have been largely applied to studies that integrate abundance

data with capture–recapture data from either individual sites or for data aggregated across sites (see Schaub and Abadi [2011] for a review). In cases where multi-site data are analyzed, failing to account for different sources of observation error could lead to biased inferences about population dynamics (Link and Sauer 1998, Ahrestani et al. 2013). The goal of this study was to develop and assess IPMs in the context of multi-site independent data sets while accounting for sampling and observation error.

IPMs can integrate data from different broad-scale avian monitoring programs, such as the North American Breeding Bird Survey (BBS; Pardieck et al. 2015) and the Monitoring Avian Productivity and Survivorship program (MAPS; Saracco et al. 2010, 2012). The BBS provides data on the status and population change of >420 bird species (Sauer and Link 2011, Sauer et al. 2014) and is a core component of continental-scale bird

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conservation efforts (e.g., Partners in Flight Species Assessment Database; *available online*).<sup>5</sup> The MAPS program provides demographic data on >100 species of landbirds (Saracco et al. 2008, DeSante and Kaschube 2009) and was designed to complement the BBS by providing data on vital rates. IPMs can incorporate key aspects of existing hierarchical models that have been developed for independent analyses of BBS and MAPS data sets. For example, IPMs can account for spatial, temporal, observer (observer identity and first survey year), and overdispersion effects in BBS count data using a state-space model (Link and Sauer 2002, Sauer and Link 2011), and for transients and random variation in recapture probability while estimating survival using a Cormack-Jolly-Seber (CJS) model (Fig. 1). Applying the IPM framework to data sets that vary with respect to the spatial scale and distribution of samples would help calibrate the BBS and MAPS data sets and potentially improve and extend inferences about demographic processes beyond the boundaries of their individual sampling areas.

Another benefit of using IPMs is their ability to estimate latent parameters (Tavecchia et al. 2009, Gimenez et al. 2012), "apparent recruitment" in the case of this study. Estimates of recruitment are important not only because they can be directly evaluated for environmental influences, but also because they allow a comparison with other vital rates, such as survival, to determine the differential influence that vital rates have on population growth. The estimates of recruitment from IPMs are not subjected to assumptions made by other models that estimate recruitment using capture–recapture data. For example, Jolly-Seber and reverse-time capture–recapture models (Pradel 1996, Link and Barker 2005) estimate recruitment without count data by not conditioning on first capture, i.e., the initial capture and the recapture probabilities are assumed to be identical. These models thus require the rather strict and more-or-less untestable assumption of "equal catchability" between marked and unmarked animals. Other disadvantages of using such capture–recapture models are their reliance on a single data set to inform both the survival and recruitment components, which may be problematic as sampling covariation and model structure can influence estimates of demographic parameters (Anderson and Burnham 1981); and that neither JS nor reverse-time models account for bias in survival or recruitment estimates associated with transients, biases that can be accounted for by hierarchical CJS components in IPMs (Pradel et al. 1997, Hines et al. 2003).

The IPM presented here is the first attempt to formally integrate MAPS and BBS data within a common modeling framework. It represents an important step for North American bird conservation by providing (1) the potential for improved estimation (increased accuracy,

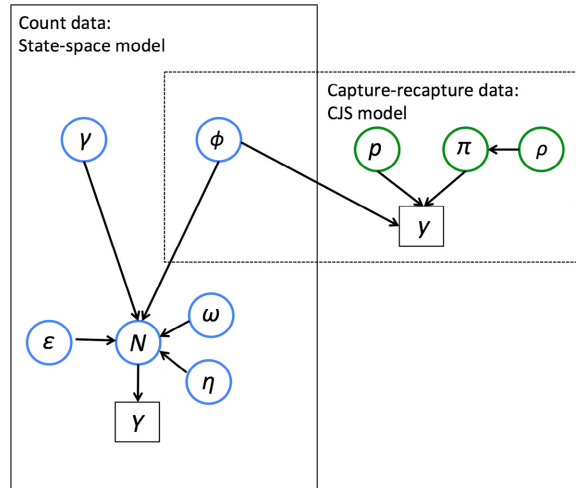


FIG. 1. Graphical representation of the population model that integrates Breeding Bird Survey (BBS) count data with capture–recapture data from the Monitoring Avian Productivity and Survivorship (MAPS) program. Parameters within blue circles ( $\gamma$ , recruitment rate;  $\phi$ , survival probability;  $N$ , index of annual population abundance;  $\omega$ , observer bias;  $\eta$ , first-year observer bias;  $\epsilon$ , observation error) were target parameters, and parameters within green circles ( $p$ , recapture probability;  $\pi$ , residency probability; and  $\rho$ , predetermining residency) were nuisance parameters (nuisance parameters here refer to parameters that are needed to describe the system, but do not have an ecological meaning). The squares represent the data ( $Y$ , BBS abundance counts;  $y$ , MAPS capture–recapture data). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

precision, resolution) of abundance, trend, and vital rates (survival, recruitment); (2) a means of assessing demographic contributions to population change based on independent data sets; (3) a framework for associating environmental covariates of population change and the demographic components of population change; and (4) estimates of latent parameters that are not directly estimable from either survey.

We used simulations to evaluate the ability of the IPM to recover parameter values. We applied the IPM to BBS and MAPS data to estimate relative abundances, demographic rates, and trends for two bird species (Gray Catbird and Wood Thrush) within the data-rich New England/Mid-Atlantic Coast Bird Conservation Region (hereafter BCR30, as defined by the North American Bird Conservation Initiative; *available online*).<sup>6</sup> Leveraging the advantage of estimating a latent parameter, in this case recruitment, we highlight the unique framework that IPMs provide to compare the influence of different vital rates on population dynamics. We also applied an overdispersed Poisson regression stand-alone BBS model (Link and Sauer 2002) and a modified MAPS stand-alone CJS model (Saracco et al. 2012) to data of both species with the intention to test whether the IPM estimates were an improvement over estimates from the stand-alone models.

<sup>5</sup> <http://rimbo.org/pifassessment/>

<sup>6</sup> <http://www.nabci-us.org/map.html>

## METHODS

*Data sources*

The MAPS program, initiated by the Institute of Bird Populations in 1989, is a cooperative network of more than 1200 field stations that use constant-effort mist netting and banding to monitor birds across the United States and Canada (DeSante and Kaschube 2009). The typical MAPS station consists of 10 12-m mist nets distributed across a core study area of approximately 8 ha and sampling birds over an area of approximately 20 ha (DeSante et al. 2004). Mist nets are operated at these stations on 6–10 days during the breeding season (see DeSante et al. 2004 for additional detail).

The North American Breeding Bird Survey (BBS) is an international avian monitoring program designed to provide relative abundance and population trend estimates for North American birds, and is jointly managed by the U.S. Geological Survey, Canadian Wildlife Service, and the Mexican National Commission for the Knowledge and Use of Biodiversity. Initiated in 1966, the BBS provides an annual index of population abundance for more than 420 bird species. Once each year, birds are counted, during the peak of the breeding season (late May or June for most regions), at points along more than 3000 road transects, referred to hereafter as “routes.” Randomly established, the routes are approximately 39.2 km long with roadside safety and access issues dictating deviations in length. The routes are surveyed by observers, skilled in avian identification, who conduct a 3-min count of birds seen within a 0.4-km radius or heard from any distance at each of 50 points separated by approximately 0.8-km intervals (Bystrak 1981, Robbins et al. 1986, Sauer et al. 2013). The total number of individuals of a species seen or heard over all 50 points per route in a given year was treated as the annual abundance count for that species on that route.

We used available capture histories for adult birds captured by the MAPS program over a 17-yr period (1992–2008) from the New England/Mid-Atlantic region, Bird Conservation Region 30 (henceforth referred to as BCR 30; see footnote 6). We matched the available MAPS data with BBS count data from the same time period, 1992–2008, and the same geographic unit, BCR 30 (details of species and the exact data analyzed can be found in *Model testing and application*).

*Integrated population model*

The IPM integrates count data with capture–recapture data by modeling the temporal dynamics of BBS counts as a first-order Markov process having survival probabilities that are simultaneously estimated from MAPS capture–recapture records (Fig. 1). Within the IPM framework, the temporal dynamics of BBS counts were modeled using a state-space model, while encounter histories from the MAPS program were modeled using a modified Cormack–Jolly–Seber model (Saracco et al. 2010).

We defined  $N_{s,t}$  as the stratum- ( $s$ ; the intersection of US states and Bird Conservation Regions (BCRs; see footnote 6) and year ( $t$ )-specific population index estimated by demographic parameters that influence the growth of a bird population within a BBS stratum. The stratum abundance in year 1,  $N_{s,1}$ , was modeled with a Poisson distribution, i.e.,  $N_{s,1} \sim \text{Pois}(\Lambda_s)$ , where  $\Lambda_s$  was the expected abundance in stratum  $s$  during year 1. Assuming exponential growth in the populations, abundance in a stratum,  $N_{s,t}$ , at time  $t > 1$  was defined to be a function of abundance at  $t - 1$ ; i.e., abundance was assumed to change as a function of a first-order Markovian process. Furthermore,  $N_{s,t}$  is assumed to be composed of two components: (1) a survival component  $S_{s,t}$ , i.e., the number of individuals that survived from the previous year; and (2) a recruitment component  $G_{s,t}$ , i.e., the number of new individuals entering the population. The combined size of these two components, i.e., the population in a given year, is represented as a function of the population size in the previous year and demographic rates (Dail and Madsen 2011)

$$\left. \begin{aligned} S_{s,t} | N_{s,t-1} &\sim \text{Bin}(N_{s,t-1}, \phi_{t-1}) \\ G_{s,t} | N_{s,t-1} &\sim \text{Pois}(\gamma_{t-1} N_{s,t-1}) \\ N_{s,t} &= S_{s,t} + G_{s,t} \end{aligned} \right\} \text{ for } t = 2, \dots, T$$

where  $\phi_t$  is the apparent annual survival probability, and  $\gamma_t$  is the apparent annual recruitment rate of the population. Note that for simplicity and for illustration of our basic model, we assume spatially constant vital rates (i.e., no  $s$  subscripts); however, stratification could be easily incorporated into  $\phi_t$  and  $\gamma_t$ . As the population surviving in a year would be a non-negative integer not greater than the maximum abundance of the previous year, we used the binomial distribution to model  $S_{s,t}$  (Schaub and Abadi 2011). Furthermore, as the apparent recruitment  $G_{s,t}$  could be any non-negative integer, it was modeled using a Poisson distribution (Besbeas et al. 2002, Kéry and Schaub 2012, Hostetler and Chandler 2015). Modeling survival and recruitment using binomial and Poisson distributions, respectively, ensured demographic stochasticity in the model.

As per standard analyses of BBS data (Link and Sauer 2002, Sauer and Link 2011), counts  $Y_{i,j,t}$  were modeled using an overdispersed Poisson regression with indexes  $i$  representing BBS route,  $t$  representing time (yr), and  $j$  representing a unique combination of route and observer. As the ability and experience of observers participating in BBS counts differ (Sauer et al. 1994, Link and Sauer 2002), the observation model of BBS counts accounts for two observer effects: (1) a normally distributed zero-mean random observer/route effect  $\omega_j$  with precision parameter  $\tau_\omega$  (where  $\tau_\omega = 1/\sigma_\omega^2$ ); (2) a fixed novice observer effect  $\eta$  (start-up-year effect) multiplied by an indicator variable  $I(j, t)$  indicating whether it's the first year ( $I(j, t) = 1$ ) or not ( $I(j, t) = 0$ ) that the observer counted on that route, and also contains normally distributed zero-mean random overdispersion effect  $\varepsilon_{i,j,t}$  with precision parameter  $\tau_\varepsilon$ .

Considering these three effects, the expected value of  $Y_{i,j,t}$ , denoted by  $\lambda_{i,j,t}$ , was modeled as

$$\log(\lambda_{i,j,t}) = \log(N_{s,t}) + \omega_j + \eta I(j,t) + \varepsilon_{i,j,t}.$$

$N_{s,t}$  is the stratum and year-specific population index of a bird population within a BBS stratum, and substitutes for the stratum-specific year effect found in the typical BBS analysis models (Link and Sauer 2002). Although observed BBS counts include observer effects and error at the scale of the route, the population index,  $N_{s,t}$ , is summarized at the scale of the stratum,  $s$ , represented here as the intersection of US states and Bird Conservation Regions (BCRs). This stratum scale summary represents the basic unit of inference for standard BBS analyses (Sauer and Link 2011) and is a convenient common area of aggregation for both BBS and MAPS data.

The estimated annual adult survival rate,  $\phi_t$ , was for resident individuals, i.e., it excludes transient individuals with zero probability of recapture after the year of marking (Pradel et al. 1997). The model assumes that the “alive state,”  $z$ , of individual  $k$  in time  $t$  is a Bernoulli process with the probability parameter equal to the product of the individual’s residency state,  $R$  ( $0 =$  transient;  $1 =$  resident), its alive state in time  $t - 1$  ( $0$ , dead or permanently emigrated;  $1$ , alive and available for capture), and the apparent survival rate,  $\phi_t$

$$z(k,t) | z(k,t-1) \sim \text{Bern}(R(k)z(k,t-1)\phi_{t-1}).$$

The residency state of newly marked individuals was determined by a residency probability parameter,  $\pi_i$ :

$$R(k) \sim \text{Bern}(\pi_{f(k)}),$$

where  $f(k)$  indicates the year of marking for individual  $k$ . Multiple within-season captures  $\geq 10$  d apart in the year of marking were used to define an observation model for residency, such that observed “pre-determined” residency, was denoted with indicator variable  $r$  ( $0$ , unknown residency status;  $1$ , observed resident) determined as a function of the residency state and probability of pre-determining an individual as a resident

$$r(k) | R(k) \sim \text{Bern}(R(k)\rho_{k,f(t)}).$$

Finally, observations of the alive state of individual  $k$  in time  $t$ ,  $c(k,t)$ , were modeled as a function of the true alive state and the recapture probability,  $p_{k,t}$ :

$$c(k,t) | z(k,t) \sim \text{Bern}(z(k,t)p_{k,t}).$$

where the  $k$  represent station-scale variation in  $p$  (see Saracco et al. 2012 for more details). We defined a logit-linear model for  $p_{k,t}$  to allow for random station-scale variation in recapture probability

$$\text{logit}(p_{k,t}) = \mu_t + \alpha_{\text{sta}[k]}$$

whereby the  $\mu_t$  represent the fixed annual mean recapture probabilities (on logit-scale) and the  $\alpha_{\text{sta}[k]}$  represent random station effects distributed as  $\text{Norm}(0, 1/\tau_\alpha)$ .

We used area-weighting (Link and Sauer 2002) to scale up the stratum-scale (BCR  $\times$  state)  $N_{s,t}$  estimates to a composite population index at the BCR level. Estimates of population growth were derived as the geometric mean of proportional annual changes of the BCR level composite population index (Link and Sauer 1998).

The apparent recruitment rate,  $\gamma_t$ , is the latent parameter estimated by the IPM, i.e., neither BBS nor MAPS empirical data provide direct estimates of recruitment. The apparent recruitment rate  $\gamma_t$  represents a compound variable, composed of four potential parameters: a fecundity rate (number of young produced per breeding adult), breeding propensity (either in terms of number of individuals breeding or the number of successful breeding attempts they have), the apparent survival probability of these juveniles, and an immigration probability (could include young, as well as dispersing adults from the previous year and other BCRs). Although data from the MAPS program could be used to inform local recruitment components, this is an area of ongoing research and is not included in the IPM presented here.

The likelihood of the state-space model ( $L_{\text{ss}}$ ) for the annual BBS counts is the product of the system process ( $L_{\text{sp}}$ ) and observation process ( $L_{\text{op}}$ ) models (Fig. 1)

$$L_{\text{ss}}(Y|N,\phi,\gamma,\omega,\eta,\varepsilon,\tau_\omega,\tau_\varepsilon) = L_{\text{op}}(Y|N,\omega,\eta,\varepsilon,\tau_\omega,\tau_\varepsilon) \\ \times L_{\text{sp}}(N|\phi,\gamma).$$

Similarly, the likelihood for the CJS model ( $L_{\text{cjs}}$ ) that relates MAPS capture–recapture data  $y$  to the apparent survival  $\phi$ , recapture  $p$ , residency  $r$ , and predetermining residency rho probabilities is

$$L_{\text{cjs}}(y|\phi,\pi,\rho,\mu,\alpha,\tau_\alpha).$$

Combining the likelihood of the state-space model for the BBS annual counts and the likelihood of the MAPS capture–recapture data would provide a joint likelihood for the overall IPM ( $L_{\text{ipm}}$ )

$$L_{\text{ipm}}(Y,y|N,\omega,\eta,\varepsilon,\tau_\omega,\tau_\varepsilon,\phi,\gamma,\pi,\rho,\mu,\alpha,\tau_\alpha) \\ = L_{\text{op}}(Y|N,\omega,\eta,\varepsilon,\tau_\omega,\tau_\varepsilon) \times L_{\text{sp}}(N|\phi,\gamma) \\ \times L_{\text{cjs}}(y|\phi,\pi,\rho,\mu,\alpha,\tau_\alpha).$$

Using Bayesian inference, the IPM (see Appendix S1 for the jags code of the IPM) was fitted to the data with the JAGS 3.3.0 (Plummer 2003) software executed using the jags function of the jagsUI package (Kellner 2015) in the R statistical computing environment (R Core Team 2016). We assigned vague prior probabilities for both survival and recruitment using uniform distributions,  $\phi_t \sim \text{U}(0,1)$  and  $\gamma_t \sim \text{U}(0,10)$ ;  $\gamma_{t,s}$  was a function of population size, and therefore had to be numerically small to enable realistic estimates of population size. The prior probability for fixed novice observer effect was modeled as  $\eta \sim \text{Norm}(0, 10^{-6})$ , while the priors for the precision hyperparameters for random observer and overdispersion effects were modeled as  $\text{Gamma}(0.001, 0.001)$ .

Posterior distributions of the demographic parameters and population size were derived from 100,000 simulated values from the posterior distribution after a burn-in of 50,000 samples of the Gibbs sampler. The Markov chains were determined to have successfully converged if R hat values were  $<1.1$  for posterior estimates of all parameters (Gelman and Hill 2006).

#### Model testing and application

We tested our model using 200 sets of simulated count and capture–recapture data. Capture–recapture histories over 10 years were simulated using the following predetermined parameter values typical for a passerine bird captured as part of the MAPS program: apparent survival  $\phi = 0.55$ , recapture probability  $p = 0.4$ , residency  $r = 0.55$ , and pre-determining residency  $\rho = 0.3$ . Abundance counts were simulated by the BBS state-space count model using the following parameter values: apparent survival  $\phi = 0.55$ ; apparent recruitment rate,  $\gamma_t = 0.5$ ; a fixed novice observer effect  $\eta = 0.2$ ; a normally

distributed zero-mean (and a SD of 0.3) random observer/route effect,  $\omega_j \sim \text{Norm}(0, 0.3)$ ; and a normally distributed zero-mean (and a SD of 0.5) random overdispersion effect,  $\varepsilon \sim \text{Norm}(0, 0.5)$  (see Appendix S2 for R code of the functions used to simulate the data).

We applied the IPM to BBS and MAPS data on populations of two bird species (Gray Catbird, *Dumetella carolinensis*, and Wood Thrush, *Hylocichla mustelina*) inhabiting BCR 30. Over the 17-yr period (1992–2008), data for Gray Catbird included capture–recapture histories of 4276 individuals captured at 38 banding stations and 1298 counts of abundance from 109 BBS routes, and the data for Wood Thrush included capture–recapture histories of 1975 individuals captured at 32 banding stations and 1379 counts of abundance from 114 BBS routes (Fig. 2). We compared the estimates from the IPM with estimates from stand-alone analyses of the BBS (using the hierarchical model described by Sauer and Link 2002) and MAPS (using CJS models), to test whether using an IPM improved precision and/or measures of central tendency in parameter estimates.

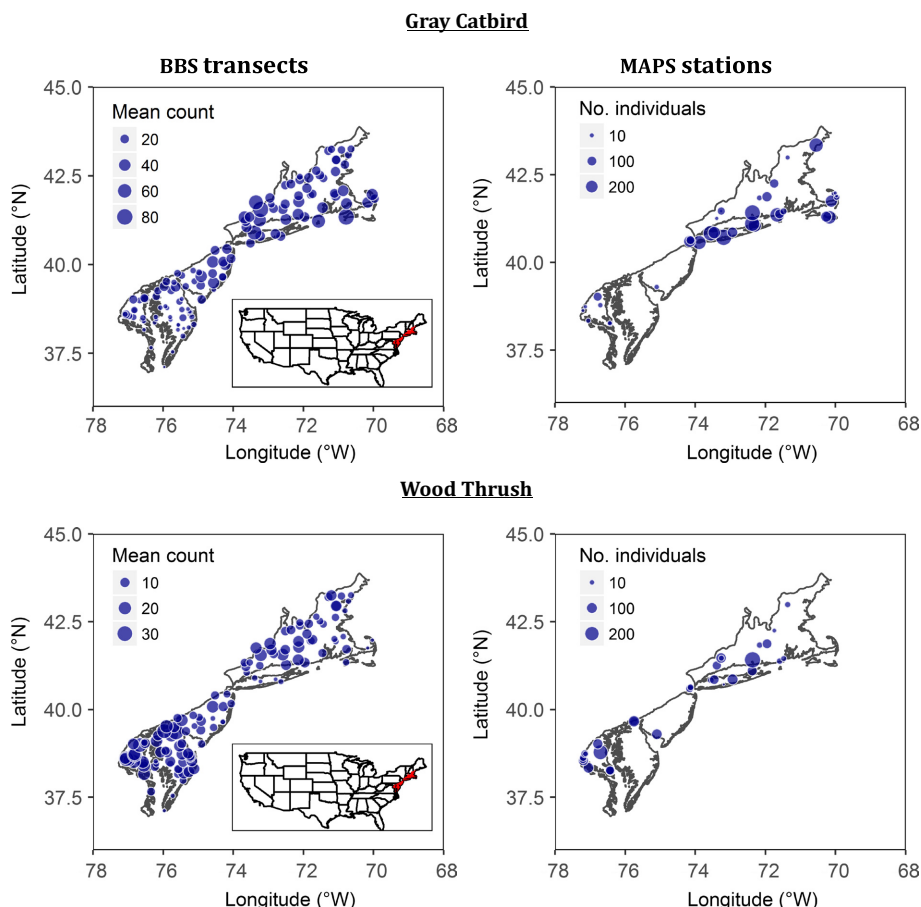


FIG. 2. The location of transects of the North American Breeding Bird Survey (BBS) and banding stations of the Monitoring for Avian Productivity and Survivorship (MAPS) program within the New England/Mid-Atlantic region, Bird Conservation Region 30, from which counts (BBS) and capture histories (MAPS) of the Gray Catbird and Wood Thrush were analyzed over the time period 1992–2008. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

RESULTS

*Simulations*

The results from testing the IPM and the CJS on 200 different sets of simulated count and capture–recapture data (all 200 data sets were simulated using the same/constant parameter values) demonstrated that the IPM accurately estimated all relevant parameters: apparent survival, recruitment, and residency probabilities and the SDs for all three effects (observer effect, novice effect, and over-dispersion effect). The simulations also confirmed that the IPM estimates of apparent recruitment were unbiased and accurate (see Appendix S3, Fig. S1).

*Application to BBS and MAPS data*

The mean and 95% Bayesian credible intervals (BCI) over the 17-yr period from the IPM and the stand-alone implementation of the CJS were similar for parameters common to both models (survival, detection, and the two residency probabilities; Table 1; see Appendix S3: Tables S1 and S2). Likewise, growth rates of the overall populations of both species in BCR 30 estimated by the IPM (Gray Catbird, mean 0.0039, 95% BCI -0.0072, 0.0153; Wood Thrush, mean -0.0484, 95% BCI -0.0599, -0.0365) were similar to growth rate estimates from the stand-alone Link and Sauer (2002) BBS model (Gray Catbird, mean 0.0004, 95% BCI -0.0089, 0.0102; Wood Thrush, mean -0.0439, 95% BCI -0.0552, -0.0269).

High variation among years over the 17-yr period was the main reason for the wide ranges of the 95% BCIs for the demographic parameters (Fig. 3). In addition to the information of survival rates provided (Table 1), the mean of the latent parameter, apparent recruitment, a compound variable that combines fecundity, juvenile survival, and immigration, was 0.42 (95% BCI 0.13, 0.75) and 0.46 (95% BCI 0.12, 0.85) over the 17-yr period for the Gray Catbird and Wood Thrush populations, respectively.

The Gray Catbird population in BCR 30 was relatively stable over the 17-yr period (mean growth rate of 0.004; 95% BCI -0.007, 0.015) with peak abundance in 1998 (Fig. 3a). The increase in Gray Catbird abundance in the 1997–1998 interval followed from the highest recruitment estimate; the year of steepest decline was 2000–2001, a period of moderate survival and low recruitment (Fig. 3a).

The mean negative growth rate (-0.05, 95% BCI -0.06, -0.04) for Wood Thrush indicates that the population has been reduced to half in BCR 30 region over the 17-yr time period, although declines were not consistent over the years (Fig. 3b). The two 1-yr intervals with the highest population increases were 1999–2000, following a year of relatively high recruitment, and 2001–2002, following a year of especially high recruitment. The year of steepest decline was 2002–2003, a result of relatively low recruitment and particularly low survival (Fig. 3b).

*Vital rate correlations and contributions to population change*

Annual apparent survival and apparent recruitment were negatively correlated for both species: posterior correlations (*r*) were -0.80 (95% BCI -0.93, -0.58) and -0.75 (95% BCI -0.90, -0.52) for the Gray Catbird and Wood Thrush populations, respectively. For Gray Catbird, annual changes in adult population size were more strongly correlated with recruitment (*r* = 0.40, 95% BCI -0.1, 0.74) than with survival (*r* = 0.10, 95% BCI -0.34, 0.55), which was similar to the pattern with the Wood Thrush population, for which changes in adult population size were also more strongly correlated with recruitment (*r* = 0.52, 95% BCI 0.12, 0.79) than with survival (*r* = 0.006, 95% BCI -0.38, 0.42).

DISCUSSION

Understanding the population dynamics of broadly distributed species and devising effective strategies for their conservation calls for large-scale collaborative monitoring efforts and appropriate analytical methods. IPMs provide a cohesive framework for analyzing independent large-scale monitoring data sets for species collected at multiple study sites across broad spatial extents (Besbeas et al. 2005, Abadi et al. 2010a, McCrea et al. 2010, Schaub and Abadi 2011). To date, there have been few applications of IPMs to such data sets, the majority of which implemented aggregated data across space, potentially biasing estimates due to error associated with the observation and sampling processes, and limiting inferences about populations to a single spatial scale (e.g., Robinson et al. 2014).

TABLE 1. The mean and 95% Bayesian credible interval (in parentheses) estimates of demographic parameters from the Integrated Population model (IPM) and a modified Cormack-Jolly-Seber model (CJS) of the Gray Catbird and Wood Thrush populations found in the New England/Mid-Atlantic region, Bird Conservation Region 30.

Probability	Gray Catbird		Wood Thrush	
	IPM	CJS	IPM	CJS
Survival	0.587 (0.368–0.827)	0.565 (0.361–0.807)	0.505 (0.286–0.787)	0.47 (0.278–0.736)
Detection	0.335 (0.197–0.514)	0.341 (0.199–0.518)	0.457 (0.217–0.712)	0.479 (0.235–0.723)
Residency	0.592 (0.415–0.821)	0.595 (0.418–0.818)	0.564 (0.365–0.837)	0.573 (0.370–0.849)
Pre-residency	0.251 (0.155–0.370)	0.249 (0.154–0.367)	0.431 (0.248–0.643)	0.425 (0.243–0.636)

Note: The IPM uses both BBS count data and MAPS capture history data, while the CJS uses only MAPS capture histories.

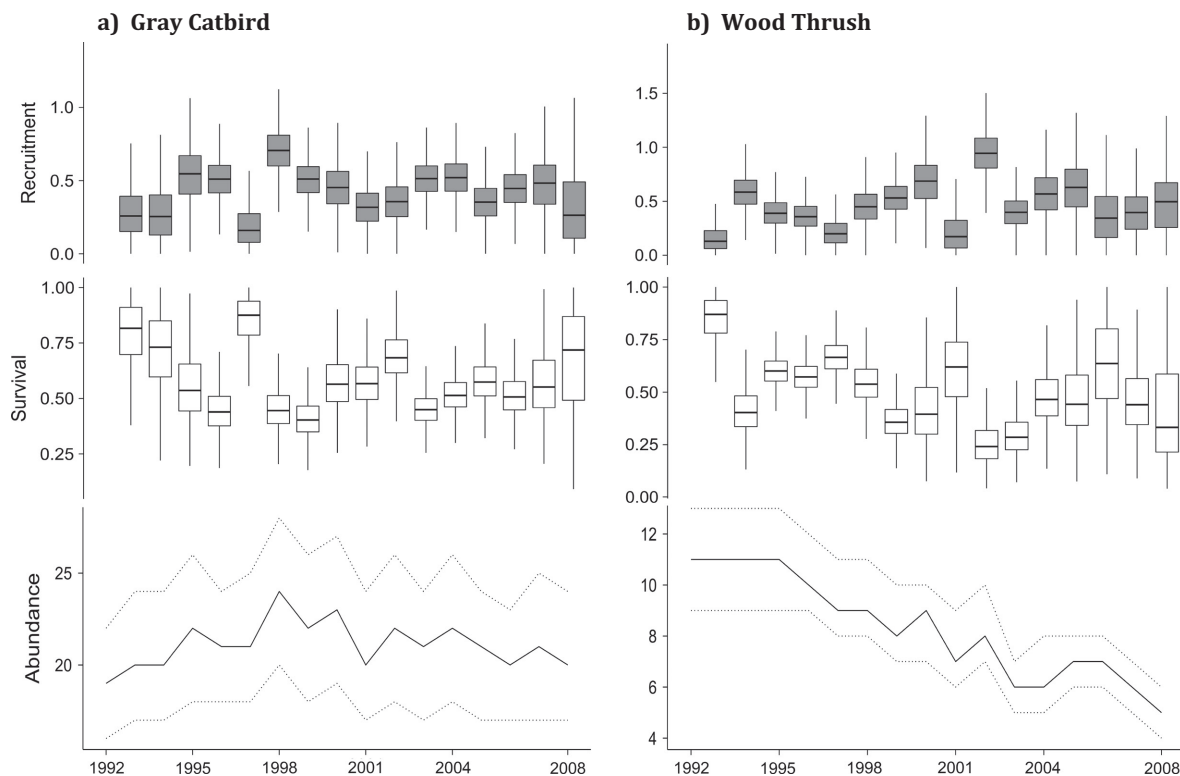


FIG. 3. Integrated Population Model (IPM) estimates of annual recruitment (shaded boxplots), annual survival (white boxplots), and trend (solid lines) in the abundance of the (a) Gray Catbird, and (b) Wood Thrush populations that inhabited BCR 30 from 1992 to 2008. The dotted lines plot the 95% credible intervals of the estimates of annual abundance. In the boxplots, boxes represent 50%, whiskers the 95% Bayesian Credible Interval, and the bars the mean of the posterior distributions. Note that there are 16 annual survival and recruitment probabilities for the 17 years of count data, beginning at  $t = 2$  (1993).

We extended the basic IPM framework to accommodate spatial and temporal observer error and overdispersion in count data, as well as accommodating spatial variation in observations among capture–recapture sites. Our model also incorporated spatial stratification in the population size index, allowing for inferences about abundance at multiple spatial scales. Such stratification could be similarly applied to the capture–recapture data in future applications of this model.

We included two important vital rate parameters in our model: adult apparent survival and apparent recruitment (DeSante 1990, Sillett and Holmes 2002). Although the recruitment parameter incorporates components of reproduction, first-year survival, and immigration, it is nevertheless an informative composite metric for evaluating the relative importance of survival and recruitment pathways, and it corresponds directly to analogous parameters in other capture–recapture models (Jolly–Seber models, reverse-time models) and population dynamics models (Royle 2004, Dail and Madsen 2011, Hostetler and Chandler 2015). With our IPM, which estimates recruitment as a latent parameter, we avoid some of the potential pitfalls (unrealistic assumptions, sampling covariation) that capture–recapture models face, and the difficulty that models that only use count data often face (insufficient information in the data; Hostetler and

Chandler 2015) while estimating recruitment (Bellier et al. 2016). Alternative parameterizations may also enable decomposition of recruitment into local and immigration components (Hostetler and Chandler 2015, Schaub and Fletcher 2015). In addition, age-specific MAPS capture data may be incorporated to allow modeling additional parameters of the recruitment pathway (e.g., productivity, first-year survival, immigration; Abadi et al. 2010b). Although sampling areas and locations differed between MAPS and BBS, we have found that demographic parameter estimates can be spatially autocorrelated across relatively large scales (e.g., Saracco et al. 2010, 2012). Thus, we suggest that demographic data from MAPS may adequately represent spatial scales larger than individual sampling areas, and that demographic parameter estimates provided by our IPM may be thought of as representing some scale intermediate between MAPS and BBS sampling scales. We suggest that future development and users of this IPM, and for that matter any other IPM, be aware that the population unit for which count data are collected may not exactly match the population unit sampled by capture–recapture methods.

A benefit of estimating the latent parameter, recruitment, was that it allows assessing the influence of vital rates on the growth of populations. In the pre-IPM era, when we could only analyze one type of data at a

time, comparing vital rates was only possible as a post-modeling process. In the case of this study, the ability of the IPM to estimate recruitment was an improvement on the stand-alone CJS model, which conditions on first capture and is therefore unable to estimate apparent recruitment (Lebreton et al. 1992). We found that, for both species, variation in annual population growth rates were associated more with variation in recruitment rates, rather than with variation in adult apparent survival. One reason for this could be that the latency of the recruitment parameter was flexed to help match the two data sets, which is why recruitment, and not survival, had a higher relation to growth in both populations. The relation of variation in annual growth with variation in recruitment was, however, stronger for the Wood Thrush than the Gray Catbird population. The importance of recruitment processes in driving population change of Wood Thrush in this region is supported by findings that non-breeding climate and breeding forest loss correlate strongly with population change in similarly defined populations of this species (see results for populations 7 and 8 in Rushing et al. [2016]).

A review of IPMs by Abadi et al. (2010a) indicated that simultaneous analysis of disparate data sets using IPMs has the potential to improve the precision of parameter estimates. We did not find, however, a gain in precision in parameter estimates from using the IPM compared to the stand-alone implementations of the CJS and BBS models. It is possible that the rich data sets available for estimating parameters overwhelmed the opportunity to improve precision of parameter estimates. Alternately, the lack of precision increase could represent a spatiotemporal mismatch in sampling between the two programs or lack of stratification in the vital rate parameters (for simplification, treated as spatially constant here).

Since its inception, the MAPS program was intended to collect demographic data that would complement abundance data from the BBS; however, until now these data sets have been treated independently. The IPM presented here represents a milestone in the evolution of both monitoring programs and should prove to be a useful tool for elucidating the dynamics of North American landbird species under a unified modeling framework. More generally, our approach represents an important step in the evolution of IPMs from applications to local populations or aggregates of populations to fully spatially stratified models that allow inferences about population dynamics at multiple scales, while accounting for spatial variation in sampling error. Other potential extensions of the model include stratification of vital rates and inclusion of additional data and parameters, inclusion of covariates to understand drivers of vital rates, and using environment-vital rate relationships to predict future population states and probabilities of quasi-extinction under various climate and land-use change scenarios.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1493/full>

## DATA AVAILABILITY

Data associated with this paper have been deposited in a Dryad digital repository: <https://doi.org/10.5061/dryad.ft64m>