Range-wide population monitoring with migration counts: a case study with Blackpoll Warbler

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**Abstract**

**Keywords** *breeding origins,* *hierarchical model, migration monitoring, population trend, stable isotopes, status assessment*

**Introduction**

North America’s boreal forest supports billions of breeding birds from more than 300 species (Niemi et al. 1998). However, increasing industrial development in this region (Hobson et al. 2013; Mahon et al. 2014), changing forest dynamics due to rapid rates of climate change (Stralberg et al. 2015), and numerous pressures during nonbreeding periods (i.e., migration, wintering; Kirby et al. 2008) have led to concern over the status of boreal avian populations. Recent studies suggest that boreal birds appear to have experienced among the steepest population declines of any avian group, owing to large declines of several previously abundant and widespread species (Rosenberg et al. 2019; 2016). There is therefore an urgent need to develop more effective avian monitoring in the boreal forest (Cumming et al. 2010)

Population trends for most North American landbirds are derived from the North American Breeding Bird Survey (BBS), but this roadside survey has limited coverage in the mostly roadless core of the boreal zone. Consequently, the BBS samples a biased collection of boreal habitats (Van Wilgenburg et al. 2015), leading to potentially unrepresentative trend estimates for boreal species (Machtans, Kardynal, and Smith 2014). Many boreal-breeding species are also migrants to neotropical regions that are not adequately monitored by nonbreeding (i.e., “wintering”) surveys such as the Christmas Bird Count (CBC). Thus, while there are substantial data with which to estimate species distributions and habitat associations (Stralberg et al. 2015; Cumming et al. 2010), range-wide trends of most boreal species are inadequately monitored (Dunn et al. 2005).

There has long been interest in counting birds during migration to evaluate population change for species that are not amenable to monitoring during the non-migratory part of their life cycle (Francis and Hussell 1998; Dunn 2005; Farmer, Hussell, and Mizrahi 2007). The Canadian Migration Monitoring Network (CMMN) represents a collaborative initiative of bird observatories across Canada, Birds Canada, and Environment and Climate Changes Canada, with an explicit goal of monitoring avian population dynamics (Crewe et al. 2008). Several long-running migration monitoring stations are also established in the United States and have provided numerous insights into the migration ecology of North America’s boreal landbirds (e.g., McNair and Nisbet 2020; Kamm et al. 2019; Miller-Rushing et al. 2008). However, one of the main limitations of using migration counts for conservation has been lack of knowledge of the breeding origins of migrants passing count stations (i.e., station catchment), and thus an inability to appropriately weight information from across a network of migration monitoring strations. Accordingly, migration monitoring data have typically been analyzed on a station-by-station basis (Crewe et al. 2016; Kamm et al. 2019), hampering attempts to evaluate range-wide population trends.

Advances in probabilistic origin assignments using stable isotopes, mainly hydrogen (δ2H), have led to cost-efficient methods for determining the origins of birds (hereafter “catchment”) including those arriving at migration monitoring stations (Hobson et al. 2015; Van Wilgenburg and Hobson 2011). Stable isotope analysis of migrants therefore facilitates an understanding of the geographic regions that are monitored by specific migration stations and provides a powerful opportunity to appropriately weight information across a network of migration monitoring stations and estimate large-scale patterns in population trends. This is particularly relevant to boreal-breeding birds that are not well-monitored by other methods, thereby delivering enhanced information for conservation decision-making.

Blackpoll Warbler (*Setophaga striata*) is an abundant Nearctic-Neotropical migrant landbird species that breeds mostly in the northern boreal forest, where breeding season surveys are extremely limited in geographic coverage. Trends derived from roadside BBS surveys suggest populations have declined by over 90% since 1970; among the steepest declines of any landbird during that period (Rosenberg et al. 2016; Sauer et al. 2017). However, the reliability of these trend estimates is uncertain owing to the absence of BBS coverage throughout the core of the species’ breeding range (Environment and Climate Change Canada 2019). Complementary monitoring methods are therefore needed for this species.

Here, we develop a Bayesian integrated population model to estimate regional and national population trends using repeated counts of migrants from a series of monitoring stations, combined with estimates of station catchments from feather stable isotope analysis. Our method synthesizes trend information at a range-wide scale by “weighting” information from migration monitoring stations based on their catchment, thereby moving beyond station-by-station analyses conducted independently. We apply this analysis to Blackpoll Warbler and compare the resulting trend estimates to those from conventional Breeding Bird Survey analysis. We also describe how this analytical framework can be readily applied to other migratory boreal species to generate estimates of range-wide population trends, and we provide fully documented R code and guidance for expanding this method to other species.

**Methods**

*Migration count data*

Our statistical model uses time series of migration counts (i.e., number of birds counted per day) collected at a network of permanent monitoring locations across Canada and the United States. The Canadian Migration Monitoring Network uses station-specific standards to collect avian counts during the pre-breeding (“spring”) and/or post-breeding (“fall”) migration seasons. Operations are daily, weather permitting, during migration seasons. The most used count approaches include banding captures using mist nets and visual counts (hereafter ‘censuses’) that record all birds detected in a specified area during a specified time. Banding is generally done for 6 hours starting a half-hour pre-dawn at fixed net locations. The length of census counts can vary from one hour (e.g., counting birds along a ‘standard’ route) to more than six hours (e.g., continuous counts from a fixed point). Count protocols vary among stations, but within a station the count methods and daily effort are standardized and remain consistent over time (Crewe et al. 2008).

For U.S. bird observatories, net locations are usually fixed, operate similar hours to those at CMMN stations, and sample at least 5 days per week during spring and/or fall migrations. However, some stations have variable daily hours and/or number of nets. Accordingly, the number of net-hours each day can be used as a statistical offset in the analysis. Models herein were developed to accommodate daily sums of standard counts for individual stations (e.g., the number of newly banded birds plus the totals from census). For our case study on Blackpoll Warbler, daily counts were available for 13 monitoring sites during pre-breeding migration and monitoring 18 sites in post-breeding migration (Table 1).

*Migration station catchment*

Our approach attempts to estimate population trends within pre-defined geographic strata, from which birds arriving at migration monitoring stations are estimated to have originated. The process of defining relevant geographic strata depends on the ability to distinguish the origins of migrants from those strata (e.g., through analysis of stable isotopes of hydrogen in feather samples from birds collected at migration monitoring stations), as well as prior knowledge of migration routes for a species of interest. For our case study of Blackpoll Warbler, we use stable isotope ratios of hydrogen (δ2H) from feathers of birds captured at migration monitoring stations to identify the likely breeding or natal origins of migrants. Blackpoll Warblers molt and produce new flight feathers prior to southward migration, thereby incorporating a biochemical “marker” of the geographic location in which their feathers were grown (Hobson 2005; Hobson et al. 2012; Holberton et al. 2015).

We defined two geographic strata (“West” and “East”) representing discrete regions of the North American boreal forest and Blackpoll Warbler breeding range (Figure 1). These strata represent regions that could be readily distinguished based on stable isotopes of hydrogen in feather samples of migrants, resulting in low uncertainty in breeding origin assignments. The boundaries of these strata are also consistent with prior knowledge of Blackpoll Warbler migration routes, based on banding, geolocator, and stable isotope studies that suggest migratory populations diverge into “east” and “west” pathways south of James Bay (DeLuca et al. 2015; Morris et al. 2016; Covino et al. 2020).

Feathers were collected from migrating Blackpoll Warblers at several migration monitoring stations during pre-breeding and post-breeding migration seasons. Sample sizes and years of data collection differed among sites. Feather samples were analyzed using methods described in Van Wilgenburg et al. (2011), yielding probabilistic estimates of the natal or breeding origins of sampled birds. The resultant breeding origin assignments, which are used as data in our statistical population model, are illustrated in Figures S2.1 and S2.2 in Appendix S2.

*Description of statistical model*

We developed a hierarchical model to estimate temporal patterns of population change within each geographic stratum. The model simultaneously estimates annual indices of bird abundance at each migration monitoring station, as well as the proportion of birds at each station that have arrived from discrete geographic strata. We fit models separately to data collected during pre-breeding migration (i.e., the northward migration of breeding birds during North American spring) and post-breeding migration (i.e., the southward migration of adult and newly fledged juvenile birds during the North American fall season).

Equations underlying the statistical model are described in Table 1. Quantities are indexed by geographic stratum (*j*), year (*y*), monitoring station (*s*), and day of year (*d*).

The highest level of the model (equation 1) describes the temporal pattern of population change in each geographic stratum *j* starting from a baseline year (the year 2000 in our analysis). Our model assumes that abundance within each stratum () changes according to a stochastic first-order Markovian process (see similar process models used in Smith et al. 2014; Sauer and Link 2011).

The next level of the model (equation 2) describes the expected number of migrants () arriving from each geographic stratum to each migration monitoring station during each year. is modeled as a product of annual stratum abundances and station-level migration parameters () that describe the contribution of stratum *j* to station *s* in year *y*. The parameters therefore convert indices of abundance in each stratum to number of birds arriving at each station in each year. We note that stratum abundances in the baseline year of the model (i.e., ) are not estimable with migration data alone, because an infinite combinations of and migration parameters ( would be equally consistent with the observed data. Thus, we fixed such that the model estimates change relative to 2000 within each stratum, ensuring all parameters are theoretically identifiable. In cases where a migration monitoring station is known (or assumed) to exclusively capture birds from a subset of strata, the relevant parameters were fixed to zero for the strata that are not monitoried by the station. For example, in our application to Blackpoll Warbler, stations located in western Canada cannot capture eastern birds because of the known migration pathways of Blackpoll Warbler and was therefore fixed to 0 for several western stations (see Table 1).

We model the index of expected annual abundance at each station () as the sum of across strata multiplied by a yearly station-specific random effect (). The term in equation 3 acknowledges that there is annual variation in the total number of migrants arriving at each station, beyond that which is attributable to changes in (e.g., additional variation could be driven by year-to-year fluctuations in migration pathways).

The next level of the model (equation 4) distributes the migrants arriving at the monitoring station among days of the season. This component of the model is necessary because some monitoring stations are only operational for a subset of days per season; the model can therefore accommodate missing data within a season. Migration of individuals past monitoring stations is assumed to follow a symmetric seasonal pattern around a peak date. We therefore described the seasonal pattern of counts at each station using a normal probability density function that integrates to 1 across all days in a season. The parameter is the date of the seasonal peak of migration at station , while describes the duration of the migration season at that station (i.e., approximately 95% of the station’s migration period occurs within 2 on either side of ). In our application of the model, was estimated separately for each migration monitoring station but was estimated as a shared parameter across stations.

The final level of the model describes the observed count data (equation 6) and breeding origin estimates (equation 7). To describe migration count data, the number of birds counted on each day of the season () at each station () in each year () was modeled as an over-dispersed Poisson process with median equal to . We assumed log-normal variance for unexplained “noise” in daily counts at each station (e.g., owing to weather conditions that affect daily migration behavior). Equation 7 also includes an offset equal to log(net hours) to account for spatio-temporal variation in monitoring effort.

Finally, we used a multinomial distribution to model breeding origins of migrants at the stations where they were collected (equation 7). In this equation, is a vector containing the number of sampled birds assigned to each of the strata at a station in a year (e.g., = [3, 17] represents a hypothetical sample of = 20 birds arriving from each of two strata, where stable isotope analysis determined that 3 birds originated from stratum 1, and 17 birds originated from stratum 2). The latent cell probabilities describing the multinomial distribution (i.e., ) therefore allow station-level dynamics to be linked to stratum-level dynamics.

**Table 1.** Multi-level statistical model to estimate population trajectories in pre-defined geographic strata by integrating daily counts of migrants at a series of monitoring stations with estimates of breeding origins for a sample of migrants at a subset of stations. Equations are indexed by geographic strata (j), year (y), monitoring station (s), and day of year (d).

|  |  |  |
| --- | --- | --- |
| Description | Equations |  |
| *Stratum-level population process model:* | | |
| Time-varying “random walk” population growth process within each stratum.  describes the magnitude of annual fluctuations in stratum-level abundance. | where: | (1) |
| *Migration process model:* | | |
| Number of migrants arriving at each station from each stratum; controlled by time-varying migration parameter |  | (2) |
| Expected number of migrants that arrive at the station during a season, from all regions. | where: | (3) |
| The expected number of migrants counted on each day of the season at a station. Seasonal temporal distribution of migrants arriving at the station follows a normal curve with a mean date and a standard deviation | , where: | (4) |
| *Observation models:* | | |
| Observed number of migrants at each station on each day of year is Poisson distributed with log-normal overdispersion (controlled by ), and an offset for survey effort (net hours). | , where: | (5) |
| Multinomial distribution describes the observed breeding origins for a sample of birds collected at a station in a given year. |  | (6) |

*Calculation of population change at regional and continental scales*

We report estimates of percent population change in a stratum (indexed by *j*) relative to a baseline year (in this study, relative to the year 2000), calculated as:

|  |  |
| --- | --- |
|  | (7) |

where is an index of abundance in the final year (), and is an index of abundance in the baseline year (). We additionally report estimates of population “trend”, which describe geometric mean rates of change between two points in time. We used the same measure of population trends applied to the North American Breeding Bird Survey (Smith et al. 2014), where:

|  |  |
| --- | --- |
|  | (8) |

Estimates of change and trend for the continental population can be calculated by summing across strata before applying equations 7 and 8. However, since our implementation of the migration model requires that (such that and are identifiable), independent estimates of relative abundance in each stratum are required in order to re-scale estimates of and thereby appropriately weight changes in abundance within each stratum at a continental scale. For example, a 1000% increase in a stratum containing only a few individuals will have a miniscule impact on continental change compared to a 10% decrease within a stratum containing the majority of the continental population.

eBird provides high-resolution rasters (2.96 km pixel width) describing model-derived predictions of relative abundance across North America during the breeding season (Fink et al. 2022). We obtained a relative abundance raster for Blackpoll Warbler using the ‘*ebirdst’* package in R, cropped this raster to the boundary of each stratum, and summed pixel values to yield estimates of relative abundance. eBird relative abundance rasters indicated that Blackpoll Warbler is currently 1.34 times more abundant in the eastern stratum than in the western stratum. We therefore re-scaled estimates of based on these values, using , where was 1.34 and 1 for the eastern and western strata, respectively.

*Parameter estimation and model diagnostics*

We fit the statistical model in a Bayesian framework using JAGS version 4.3.0, interfaced with the R programming language version 4.0.2 using the jagsUI library. We specified vague priors on all model parameters; see Appendix 1 for details of prior specification. After a burn-in of 10,000 iterations, we stored every 100th iteration until we accumulated 1000 posterior samples from each of three MCMC chains. We assessed chain convergence by visual examination of MCMC traceplots and by evaluating that the Gelman–Rubin convergence statistic was close to 1 for all model parameters.

We assessed goodness-of-fit by evaluating the correlations between observed seasonal totals at monitoring stations and the expected counts generated by the fitted models. We also conducted posterior predictive checks to confirm that the distribution of simulated counts based on the fitted statistical model were consistent with the distribution of observed counts at each station.

Finally, we used simulations to evaluate whether the migration model was able to generate unbiased estimates of regional population trends across a wide range of regional trajectory scenarios, and to evaluate the degree to which trend estimates were improved by repeatedly conducting stable isotope analyses at migration monitoring stations. Simulation methods are fully described in Appendix 3.

*Comparison to trend estimates from the North American Breeding Bird Survey*

We compared regional trend estimates from our model to those derived from the North American Breeding Bird survey, to evaluate differences between conventional breeding season analyses and our migration analysis. We fit a Bayesian hierarchical model to BBS time series from 2008 to 2018 (the same period as our migration analysis), using analytical strata implemented by the United States Geological Survey (USGS) for continental analysis. We specified a “first difference” population process model (Link, Sauer, and Niven 2017; Smith and Edwards 2021), which is widely used in standard continental analysis of BBS data. We fit the model and extracted output using the ‘bbsBayes’ package in R (Edwards and Smith 2020), specifying a 50,000 iteration burn-in period, after which we stored every 100th posterior sample until we accumulated 2000 posterior samples from each of 3 MCMC chains.

We calculated estimates of continental change based on analysis of the BBS, using methods described in Link, Sauer, and Niven (2017) and Smith and Edwards (2021). To derive regional trend estimates from the BBS, we assigned BBS analytical strata into “east” and “west” categories based on geographic overlap with the strata we used for migration analysis (Figure S1 in Appendix 2). This allowed us to calculate “post hoc” synthetic estimates of regional population trends by summing annual indices from the fitted model across analytical strata that overlapped with the coarse east and west strata used for the migration monitoring analysis. Detailed methods for estimating population trajectories and trends within custom strata are described in the bbsBayes package, available at <https://github.com/bbsBayes/bbsBayes> (Edwards and Smith 2020).

**Results**

Simulations confirmed that the statistical model produces regional trend estimates that are identifiable and unbiased under a wide range of simulated population trajectories and data collection scenarios. Simulations also showed that regional population trends can be estimated more precisely when feather isotope samples were collected repeatedly through time at migration monitoring stations. Collecting feathers every 5 years resulted in regional trend estimates that were 22% more precise (measured as width of the 95% credible intervals) than if feather samples were collected once at each station (Table S5.1; Figure S5.5). When feather samples were collected every year along with migration counts, trend estimates were 46% more precise than if feather samples were only collected once.

For our empirical case study of Blackpoll Warbler, we detected weak evidence of large population changes (i.e., doubling or halving of population size) in western North America between 2000 and 2018 (Table 2; left column of Figure 2). Furthermore, 95% credible intervals on population trends from both sources of migration monitoring information (pre-breeding and post-breeding migration) broadly overlapped zero, and were consistent with the regional trend estimate from the BBS which also overlapped zero. Estimates of population trend and overall percent change based on migration monitoring were less precise than those from the BBS, but all three estimates were relatively imprecise (e.g., 95% credible intervals included declines of more than 30% and simultaneously increases of more than 50%).

Pre-breeding migration and BBS both suggested that Blackpoll Warbler populations had likely occurred in eastern North America since 2000 (Table 2; right column of Figure 2). Pre-breeding migration indicated there was close to a 100% chance declines had occurred, and a 91% chance that the population had declined by more than 50%. BBS also suggested there was a 98% chance the population had declined, but the magnitude of decline was lower than that from pre-breeding migration (21% chance the population had declined by more than 50%). Trend estimates from BBS were also much more precise than those from pre-breeding migration. Trends and population trajectories estimated from post-breeding migration were too imprecise for useful comparisons to other monitoring data; this was because few stations captured large numbers of eastern migrants during post-breeding migration (Figure S2.2), and signals of eastern population changes were largely swamped by migrants originating from the western stratum.

Pre-breeding migration monitoring and BBS yielded strong evidence for continental population declines between 2000 and 2018 (Table 2), primarily due to declines in eastern North America. However, BBS trends were less negative than those from pre-breeding migration and suggested low evidence (less than 1% chance) that the continental population had declined by more than 50%, while pre-breeding migration suggested there was moderate evidence (78% chance) the population had halved. Continental change estimates from post-breeding migration were too imprecise to be useful, owing to the extreme imprecision in eastern population estimates.

The migration model also produces estimates of annual indices of abundance at each migration monitoring station, and associated estimates of the regional composition of migrating birds in each year of study. Station-level estimates of annual indices are presented in Appendix 6.

**Discussion**

**Paragraph 1:**

**Paragraph 2:**

**Paragraph 3:**

**Paragraph 4:**

**Paragraph 6:**

**Authors’ Contributions**

All authors conceived of research ideas. EHD and DE compiled and cleaned migration count data. SVW and KJK conducted statistical analyses of feather isotopes to determine breeding origins. DTI developed statistical model, led analysis, and wrote the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication. **EHD was extremely patient while DTI spent several years trying to wrap his head around the modeling.**

**Data Accessibility**

Canadian migration count data are publicly available at the NatureCounts portal (https://www.bsc-eoc.org/birdmon/cmmn/datasets.jsp), managed by Birds Canada. US migration counts are available upon request from individual migration monitoring stations. All isotope data, code, and Bayesian posterior samples associated with these analyses will be archived in Dryad Digital Repository upon acceptance of this manuscript.

**Conflict of Interest**

The authors declare they have no conflict of interest.

**Compliance with Ethical Standards**

The authors declare that they have complied with ethical standards.

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