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, model-derived annual indices of abundance at migration monitoring stations and their associated regional composition are depicted in Figures XX and XX. Our analysis suggested that the western population stratum was monitored by several migration stations in both the pre-breeding and post-breeding migration periods (Figures S2.1 and S2.2). In contrast, few stations captured substantial numbers of ‘eastern’ Blackpoll Warblers during post-breeding migration. Accordingly, eastern population trajectories estimated from post-breeding migration were highly imprecise and poorly estimated, because signals of eastern population changes were largely swamped by migrants originating from the western stratum.

In combination, analysis of migration monitoring data and BBS indicated that Blackpoll Warbler populations in western North America were unlikely to have declined substantially from 2000 to 2018 (left column of Figure 2). All three sources of monitoring (pre-breeding migration, post-breeding migration, and BBS) yielded comparable estimates of population change in western North America (Table 2).

In contrast to results for the western population stratum, eastern population trend estimates differed among the three sources of monitoring. Pre-breeding migration suggested that eastern populations strongly declined between 2000 and 2018. Trend estimates from the BBS suggested that eastern populations have likely declined, but less steeply than estimated from pre-breeding migration. Estimates of eastern population trends based on post-breeding migration were too imprecise to make meaningful comparisons to other monitoring programs, owing to the lack of a large eastern catchment at any stations.

Pre-breeding migration monitoring yielded strong evidence for continental population declines between 2000 and 2018, primarily due to declines detected in the eastern stratum. However, continental trend estimates based on post-breeding migration were extremely imprecise owing to imprecision in estimates for the eastern stratum, precluding useful comparisons to other sources of information. The BBS suggested there was weak evidence of continental population declines between 2000 and 2018.

**Discussion**

**Migration monitoring provides a potentially powerful way to monitor boreal birds. BBS and migration monitoring**

**Less precise than BBS – reasons.**

**Repeated sampling of isotopes.**

**More precise estimates of catchments.**

* **Many stations lack isotope information. Model yields testable predictions.**
* **More monitoring stations during fall migration, but less precise estimates**
  + **Loop migration of blackpoll warbler**
  + **Lack of catchment information**
* **Recommendations for future monitoring: repeated isotope sampling at stations where catchment is mixed. Repeated sampling of isotopes provides trend information.**

Using a novel statistical model, we estimated regional population trends migration monitoring data. Applying this model to a boreal breeding songbird revealed more optimistic 10-year national trend estimates than those derived from Breeding Bird Surveys that are largely collected at the periphery of the species range. Estimates derived from the BBS suggest that blackpoll warblers comprise 10% (307 million) of the estimated 3 billion breeding birds across all species that no longer exist in North America relative to 1970 (see Data S1 in Rosenberg et al. 2019). Accordingly, the blackpoll warbler is considered a common bird in steep decline and a priority for ongoing monitoring and conservation (Rosenberg et al. 2016). Our analysis suggests that steep population declines are unlikely to have occurred nationally across the three most recent generations for this species, and that there is a low probability blackpoll warbler currently meets COSEWIC criteria for Threatened status designation.

Our findings are consistent with ecological theorythat predicts population trends are less positive at species range margins, where habitat quality is lower and environmental conditions are further from a species’ optimum (MacArthur 1984; Hargreaves, Samis, and Eckert 2014). Theory also predicts that species will be more sensitive to environmental change at range margins, though empirical evidence for this prediction is mixed (Amburgey et al. 2018; Kleinhesselink and Adler 2018; Iles et al. 2020). The North American Breeding Bird Survey, as a roadside survey, contains large spatial gaps in the core of the roadless boreal forest and therefore primarily samples the periphery of boreal species’ ranges. This spatial bias leads to an unrepresentative sample of boreal habitats and anthropogenic disturbance, which is more severe near inhabited roadside areas (Van Wilgenburg et al. 2015; Dunn et al. 2005). If BBS surveys are restricted to the periphery of a species range, and in disproportionately disturbed habitats, trends derived from the BBS will be more negative than methods that survey the core of the range. Indeed, a long-term study of 50 species at an intact boreal study site found that population trends were on average more positive than regional and national BBS trends (Machtans, Kardynal, and Smith 2014). Our national migration trends were also more positive than BBS trends, which is consistent with this hypothesis; the migration monitoring network likely captures individuals from across the entire boreal range (Hobson et al. 2015; Dunn 2005) rather than disproportionately monitoring populations at range margins.

Climate-driven range shifts could also lead to the discrepancy we identified between trends based on breeding and migration surveys. In the case of the Breeding Bird Survey, a northward shift in population range for boreal-breeding species could masquerade as spurious population declines, given that most BBS survey locations are largely restricted to the southern periphery of the Canadian boreal forest. Thus, individuals shifting northward out of the BBS sampling frame would appear as a population decline, even if abundance were stable nationally. Recent evidence suggests that a 600 km northward shift in blackpoll warbler breeding range has likely occurred over the last 45 years (Gómez et al. 2021), coinciding with the period during which trends derived from BBS have been highly negative. In this case, migration monitoring may be more robust to climate-driven range shifts because populations that have shifted their breeding locations will nevertheless continue to be surveyed during their migration.

Migration analysis yielded short-term national trend estimates that had similar precision to those from the BBS, but a lack of historical migration counts and stable isotope data precluded usefully precise long-term estimates of population performance from migration monitoring (i.e., prior to 2008). We therefore cannot compare migration-based trend analysis to those from breeding surveys during the period in which the steepest population declines appear to have occurred for this species. Nevertheless, application of our method to other boreal breeding species would provide a strong test of the hypothesis that BBS-derived trends are overly pessimistic for species experiencing northward range shifts and/or species with large populations in the roadless core of the boreal forest. Simultaneously, our analytical approach could provide valuable insights for other groups of birds that are more reliably covered on migration or at stopover sites, such as shorebirds and raptors (Farmer, Hussell, and Mizrahi 2007), for which BBS-derived trend estimates are highly uncertain.

Independent estimates of abundance within each analytical stratum are required to properly “weight” regional trajectories and produce a national trajectory (see *Converting Regional Trajectories from Migration Monitoring into Regional Population Sizes* in *Methods* section*)*. For North American landbirds, considerable progress has been made towards understanding the relative strengths and limitations of different datasets used for this purpose (Sólymos et al. 2020; Thogmartin 2010; Confer et al. 2008). Our analysis relied on population abundance estimates produced from boosted regression trees trained on hundreds of thousands of avian point counts collected across the Canadian boreal forest (Stralberg et al. 2015; Boreal Avian Modeling Project 2020), with explicit corrections for variation in survey methodology among observations (Sólymos et al. 2013). New efforts to deploy a rigorously designed national sampling protocol across the entire Canadian boreal forest also hold immense promise for producing improved estimates of landbird densities (Van Wilgenburg et al. 2020), that can be used to both test predictions from our model and generate improved model outputs.

Possibly insert a paragraph about the east/west gradient that appears to occur in both the migration and BBS data?

* Causes of this gradient? Things to discuss?
* Somewhat worried that the discussion is too “blackpollish”, and not general enough. Adding this paragraph would make the paper even more species-specific. Thoughts/advice?

The current formulation of our model assumes that migration pressure is constant through time (i.e., has no temporal component; Table 1) and that directional changes in abundance of migrants are due to changes in regional population sizes, rather than directional shifts in migration routes. Repeated sampling of migrants for stable isotopes at multiple stations could be used to evaluate whether station catchment is changing over time and would allow for temporal components to be added to the terms. Importantly, our model makes explicit predictions about the proportion of migrants from each region in a station’s annual catchment (equations 2, 3, and 7). Iteratively confronting predictions with new data is the strongest test of scientific theory and the fastest way to improve ecological understanding (Dietze et al. 2018), and we therefore consider the collection of new stable isotope data across the migration network a priority for further model testing and refinement.

Moving forward, our model could potentially be extended to incorporate non-standardized migration count data from citizen science networks such as eBird (Sullivan et al. 2014), conceptually equivalent to adding thousands of migration monitoring “stations” across the continent. This would have numerous advantages including more comprehensive coverage of migratory populations and reducing the influence of any single migration monitoring station on regional trend estimates. However, reliance on citizen science information requires careful screening of data and appropriate accounting of changes in observer effort over time (e.g., through modeling). For migration monitoring, this also requires limiting data to locations outside breeding and/or wintering areas to avoid confounding changes in migrant numbers with signals of change in local numbers of seasonal residents. Simultaneously, the continual improvement of wildlife tracking technologies will undoubtedly yield finer resolution estimates of migration behaviour, and thus, station catchment. Future integrated analysis of these data would allow trends to be estimated in a larger number of higher resolution strata, yielding enhanced information at conservation-relevant scales.

Interpretation of station-level trends is also complicated by the “loop migration” behaviour of blackpoll warblers, wherein populations follow very different migration routes during spring and fall (Holberton et al. 2015; Covino et al. 2020; DeLuca et al. 2019). A single station may therefore be monitoring birds originating from different origins of the breeding range during each migration season. Furthermore, most of the continental population appears to congregate along the northeast coast of the United States during fall migration, prior to undertaking a transoceanic flight to nonbreeding areas in South America (Holberton et al. 2015; DeLuca et al. 2015; Nisbet et al. 1995). Thus, stations in this region are likely to capture a mixture of birds from across the breeding range.

**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.

**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.

**References**

Amburgey, Staci M., David A. W. Miller, Evan H. Campbell Grant, Tracy A. G. Rittenhouse, Michael F. Benard, Jonathan L. Richardson, Mark C. Urban, et al. 2018. “Range Position and Climate Sensitivity: The Structure of among-Population Demographic Responses to Climatic Variation.” *Global Change Biology* 24: 439–54. https://doi.org/10.1111/gcb.13817.

Birds Canada. 2020. “NatureCounts - Canadian Migration Monitoring Network.” 2020. https://www.birdscanada.org/birdmon/cmmn/popindices.jsp?what=trendmaps.

Boreal Avian Modeling Project. 2020. “New Canada-Wide Land Bird Density Estimates (Version 4.0).” The Boreal Avian Modelling Project. 2020. https://borealbirds.ualberta.ca/maps-data/data-products-2/new-canada-wide-land-bird-density-estimates-version-4/.

Che-Castaldo, Christian, Stephanie Jenouvrier, Casey Youngflesh, Kevin T. Shoemaker, Grant Humphries, Philip McDowall, Laura Landrum, Marika M. Holland, Yun Li, and Rubao Ji. 2017. “Pan-Antarctic Analysis Aggregating Spatial Estimates of Adélie Penguin Abundance Reveals Robust Dynamics despite Stochastic Noise.” *Nature Communications* 8: 832. https://doi.org/10.1038/s41467-017-00890-0.

Confer, John L., Rebecca E. Serrell, Mark Hager, and Eleanor Lahr. 2008. “Field Tests of the Rosenberg-Blancher Method for Converting Point Counts to Abundance Estimates.” *The Auk* 125 (4): 932–38.

Covino, Kristen, Sara Morris, Mark Shieldcastle, and Philip Taylor. 2020. “Spring Migration of Blackpoll Warblers across North America.” *Avian Conservation and Ecology* 15 (1).

Crewe, Tara L., Jon D. McCracken, Philip D. Taylor, Denis Lepage, and Audrey E. Heagy. 2008. “The Canadian Migration Monitoring Network-Réseau Canadien de Surveillance Des Migrations: Ten-Year Report on Monitoring Landbird Population Change.” *CMMN-RCSM Scientific Technical Report* 1.

Cumming, Steven G., E. Bayne, F. K. A. Schmiegelow, Trish Fontaine, S. J. Song, and K. Lefevre. 2010. “Toward Conservation of Canada’s Boreal Forest Avifauna: Design and Application of Ecological Models at Continental Extents.”

DeLuca, William V., Bradley K. Woodworth, Stuart A. Mackenzie, Amy EM Newman, Hilary A. Cooke, Laura M. Phillips, Nikole E. Freeman, Alex O. Sutton, Lila Tauzer, and Carol McIntyre. 2019. “A Boreal Songbird’s 20,000 Km Migration across North America and the Atlantic Ocean.” *Bulletin of the Ecological Society of America* 100 (3): 1–5.

DeLuca, William V., Bradley K. Woodworth, Christopher C. Rimmer, Peter P. Marra, Philip D. Taylor, Kent P. McFarland, Stuart A. Mackenzie, and D. Ryan Norris. 2015. “Transoceanic Migration by a 12 g Songbird.” *Biology Letters* 11 (4): 20141045.

Dietze, Michael C., Andrew Fox, Lindsay M. Beck-Johnson, Julio L. Betancourt, Mevin B. Hooten, Catherine S. Jarnevich, Timothy H. Keitt, Melissa A. Kenney, Christine M. Laney, and Laurel G. Larsen. 2018. “Iterative Near-Term Ecological Forecasting: Needs, Opportunities, and Challenges.” *Proceedings of the National Academy of Sciences* 115: 1424–32. https://doi.org/10.1073/pnas.1710231115.

Dunn, Erica H. 2005. “Counting Migrants to Monitor Bird Populations: State of the Art.” *USDA Forest Service General Technical Report PSW-GTR-191*, 712–17.

Dunn, Erica H., B. L. Altman, J. Bart, C. J. Beardmore, H. Berlanga, P. J. Blancher, G. S. Butcher, D. W. Demarest, R. Dettmers, and W. C. Hunter. 2005. *High Priority Needs for Range-Wide Monitoring of North American Landbirds*. Partners in Flight Technical Series 2. Partners in Flight.

Edwards, Brandon PM, and Adam C. Smith. 2020. “BbsBayes: An R Package for Hierarchical Bayesian Analysis of North American Breeding Bird Survey Data.” *BioRxiv*.

Environment and Climate Change Canada. 2019. “Blackpoll Warbler.” Status of Birds in Canada. 2019. https://wildlife-species.canada.ca/bird-status/oiseau-bird-eng.aspx?sY=2019&sL=e&sM=a&sB=BLPW.

Farmer, Christopher J., David JT Hussell, and David Mizrahi. 2007. “Detecting Population Trends in Migratory Birds of Prey.” *The Auk* 124 (3): 1047–62.

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, S. Ligocki, O. Robinson, W. Hochachka, L. Jaromczyk, A. Rodewald, C. Wood, I. Davies, A. Spencer. 2022. eBird Status and Trends, Data Version: 2021; Released: 2022. Cornell Lab of Ornithology, Ithaca, New York. <https://doi.org/10.2173/ebirdst.2021>

Francis, C. M., and D. J. T. Hussell. 1998. “Changes in Numbers of Land Birds Counted in Migration at Long Point Bird Observatory, 1961-1997.” *Bird Populations* 4: 37–66.

Gómez, Camila, Keith A. Hobson, Nicholas J. Bayly, Kenneth V. Rosenberg, Andrea Morales-Rozo, Paula Cardozo, and Carlos Daniel Cadena. 2021. “Migratory Connectivity Then and Now: A Northward Shift in Breeding Origins of a Long-Distance Migratory Bird Wintering in the Tropics.” *Proceedings of the Royal Society B* 288 (1948): 20210188.

Hargreaves, Anna L., Karen E. Samis, and Christopher G. Eckert. 2014. “Are Species’ Range Limits Simply Niche Limits Writ Large? A Review of Transplant Experiments beyond the Range.” *The American Naturalist* 183 (2): 157–73.

Hobson, K. A. (2005). Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *The Auk*, *122*(4), 1037-1048.

Hobson, Keith, Steven L. Van Wilgenburg, Erica Dunn, David Hussell, Philip Taylor, and Douglas Collister. 2015. “Predicting Origins of Passerines Migrating through Canadian Migration Monitoring Stations Using Stable-Hydrogen Isotope Analyses of Feathers: A New Tool for Bird Conservation.” *Avian Conservation and Ecology* 10 (1).

Hobson, Keith, Amy Wilson, Steven L. Van Wilgenburg, and Erin Bayne. 2013. “An Estimate of Nest Loss in Canada Due to Industrial Forestry Operations.” *Avian Conservation and Ecology* 8 (2).

Holberton, Rebecca L., Steven L. Van Wilgenburg, Adrienne J. Leppold, and Keith A. Hobson. 2015. “Isotopic (Δ2Hf) Evidence of ‘Loop Migration’ and Use of the Gulf of Maine Flyway by Both Western and Eastern Breeding Populations of Blackpoll Warblers.” *Journal of Field Ornithology* 86 (3): 213–28.

Hooten, Mevin B., and N. Thompson Hobbs. 2015. “A Guide to Bayesian Model Selection for Ecologists.” *Ecological Monographs* 85 (1): 3–28.

Iles, David T., Heather Lynch, Rubao Ji, Christophe Barbraud, Karine Delord, and Stephanie Jenouvrier. 2020. “Sea Ice Predicts Long‐term Trends in Adélie Penguin Population Growth, but Not Annual Fluctuations: Results from a Range‐wide Multiscale Analysis.” *Global Change Biology* 26 (7): 3788–98.

Kamm, Matthew D., Trevor L. Lloyd-Evans, Maina Handmaker, and J. Michael Reed. 2019. “A Half-Century of Changes in Migratory Landbird Numbers along Coastal Massachusetts.” *PloS One* 14 (9): e0222232.

Kleinhesselink, Andrew R, and Peter B Adler. 2018. “The Response of Big Sagebrush (Artemisia Tridentata) to Interannual Climate Variation Changes across Its Range.” *Ecology* 99: 1139–49. https://doi.org/10.1002/ecy.2191.

Koons, David N., David T. Iles, Michael Schaub, and Hal Caswell. 2016. “A Life‐history Perspective on the Demographic Drivers of Structured Population Dynamics in Changing Environments.” *Ecology Letters* 19: 1023–31. https://doi.org/10.1111/ele.12628.

Link, William A., John R. Sauer, and Daniel K. Niven. 2017. “Model Selection for the North American Breeding Bird Survey: A Comparison of Methods.” *The Condor: Ornithological Applications* 119 (3): 546–56.

MacArthur, Robert H. 1984. *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press.

Machtans, Craig, Kevin Kardynal, and Paul Smith. 2014. “How Well Do Regional or National Breeding Bird Survey Data Predict Songbird Population Trends at an Intact Boreal Site?” *Avian Conservation and Ecology* 9 (1).

Mahon, C. Lisa, Erin M. Bayne, Péter Sólymos, Steven M. Matsuoka, Matthew Carlson, Elston Dzus, Fiona KA Schmiegelow, and Samantha J. Song. 2014. “Does Expected Future Landscape Condition Support Proposed Population Objectives for Boreal Birds?” *Forest Ecology and Management* 312: 28–39.

McNair, Douglas B., and Ian CT Nisbet. 2020. “Status and Abundance of Blackpoll Warblers in Autumn on the Coast of the Southeastern United States: An Update.” *Southeastern Naturalist* 19 (2): 241–55.

Miller-Rushing, A.J., T.L. Lloyd-Evans, Richard B. Primack, and Paul Satzinger. 2008. “Bird Migration Times, Climate Change, and Changing Population Sizes.” *Global Change Biology* 14 (9): 1959–72.

Morris, S. R., Covino, K. M., Jacobs, J. D., & Taylor, P. D. (2016). Fall migratory patterns of the Blackpoll Warbler at a continental scale. *The Auk: Ornithological Advances*, *133*(1), 41-51.

Niemi, Gerald, JoAnn Hanowski, Pekka Helle, Robert Howe, Mikko Mönkkönen, Lisa Venier, and Daniel Welsh. 1998. “Ecological Sustainability of Birds in Boreal Forests.” *Conservation Ecology* 2 (2).

Nisbet, Ian CT, Douglas B. McNair, William Post, and Timothy C. Williams. 1995. “Transoceanic Migration of the Blackpoll Warbler: Summary of Scientific Evidence and Response to Criticisms by Murray (Migración Transoceánica de Dendroica Striata: Resumen de Investigaciones y Respuesta a La Crítica de Murray).” *Journal of Field Ornithology*, 612–22.

Ralston, Joel, and Jeremy J. Kirchman. 2012. “Continent-Scale Genetic Structure in a Boreal Forest Migrant, the Blackpoll Warbler (Setophaga Striata).” *The Auk* 129 (3): 467–78.

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, and G. S. Butcher. 2016. “Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States.” *Partners in Flight Science Committee* 35.

Rosenberg, K.V., Adriaan M. Dokter, Peter J. Blancher, John R. Sauer, Adam C. Smith, Paul A. Smith, Jessica C. Stanton, Arvind Panjabi, Laura Helft, and Michael Parr. 2019. “Decline of the North American Avifauna.” *Science* 366 (6461): 120–24.

Sauer, John, Daniel Niven, James Hines, David Ziolkowski Jr, Keith L. Pardieck, J. E. Fallon, and William Link. 2017. “The North American Breeding Bird Survey, Results and Analysis 1966-2015.”

Sauer, John R., and William A. Link. 2011. “Analysis of the North American Breeding Bird Survey Using Hierarchical Models.” *The Auk* 128 (1): 87–98.

Smith, Adam C., and Brandon PM Edwards. 2021. “North American Breeding Bird Survey Status and Trend Estimates to Inform a Wide Range of Conservation Needs, Using a Flexible Bayesian Hierarchical Generalized Additive Model.” *The Condor* 123 (1): duaa065.

Smith, Adam C., Marie-Anne R. Hudson, Constance Downes, and Charles M. Francis. 2014. “Estimating Breeding Bird Survey Trends and Annual Indices for Canada: How Do the New Hierarchical Bayesian Estimates Differ from Previous Estimates?” *The Canadian Field-Naturalist* 128 (2): 119–34.

Sólymos, Péter, Steven M. Matsuoka, Erin M. Bayne, Subhash R. Lele, Patricia Fontaine, Steve G. Cumming, Diana Stralberg, Fiona KA Schmiegelow, and Samantha J. Song. 2013. “Calibrating Indices of Avian Density from Non‐standardized Survey Data: Making the Most of a Messy Situation.” *Methods in Ecology and Evolution* 4 (11): 1047–58.

Sólymos, Péter, Judith D Toms, Steven M Matsuoka, Steven G Cumming, Nicole K S Barker, Wayne E Thogmartin, Diana Stralberg, et al. 2020. “Lessons Learned from Comparing Spatially Explicit Models and the Partners in Flight Approach to Estimate Population Sizes of Boreal Birds in Alberta, Canada.” *The Condor* 122 (2). https://doi.org/10.1093/condor/duaa007.

Stralberg, D., S. M. Matsuoka, A. Hamann, E. M. Bayne, P. Sólymos, F. K. A. Schmiegelow, X. Wang, S. G. Cumming, and S. J. Song. 2015. “Projecting Boreal Bird Responses to Climate Change: The Signal Exceeds the Noise.” *Ecological Applications* 25 (1): 52–69.

Sullivan, Brian L., Jocelyn L. Aycrigg, Jessie H. Barry, Rick E. Bonney, Nicholas Bruns, Caren B. Cooper, Theo Damoulas, André A. Dhondt, Tom Dietterich, and Andrew Farnsworth. 2014. “The EBird Enterprise: An Integrated Approach to Development and Application of Citizen Science.” *Biological Conservation* 169: 31–40.

Thogmartin, Wayne E. 2010. “Sensitivity Analysis of North American Bird Population Estimates.” *Ecological Modelling* 221 (2): 173–77.

Tredennick, Andrew T., Giles Hooker, Stephen P. Ellner, and Peter B. Adler. 2021. “A Practical Guide to Selecting Models for Exploration, Inference, and Prediction in Ecology.” *Ecology* 102 (6): e03336. https://doi.org/10.1002/ecy.3336.

Van Wilgenburg, Steven L., Elizabeth Beck, Brennan Obermayer, Timothy Joyce, and Brett Weddle. 2015. “Biased Representation of Disturbance Rates in the Roadside Sampling Frame in Boreal Forests: Implications for Monitoring Design.” *Avian Conservation and Ecology* 10 (2).

Van Wilgenburg, Steven L., and Keith A. Hobson. 2011. “Combining Stable‐isotope (ΔD) and Band Recovery Data to Improve Probabilistic Assignment of Migratory Birds to Origin.” *Ecological Applications* 21 (4): 1340–51.

Van Wilgenburg, Steven L., C. Lisa Mahon, Greg Campbell, Logan McLeod, Margaret Campbell, Dean Evans, Wendy Easton, Charles M. Francis, Samuel Haché, and Craig S. Machtans. 2020. “A Cost Efficient Spatially Balanced Hierarchical Sampling Design for Monitoring Boreal Birds Incorporating Access Costs and Habitat Stratification.” *Plos One* 15 (6): e0234494.