A model for estimating range-wide population trend based on migration counts: a case study with Blackpoll Warbler (*Setophaga striata*)

David T. Iles1, Erica H. Dunn2, Steven Van Wilgenburg3, Kevin J. Kardynal4, Danielle Ethier5, Adam C. Smith1, Charles M. Francis1

1 Canadian Wildlife Service, Environment and Climate Change Canada, Ottawa, ON, Canada

2 Canadian Migration Monitoring Network, Birds Canada, Port Rowan, ON, Canada

3 Canadian Wildlife Service, Environment and Climate Change Canada, Saskatoon, SK, Canada

4 Wildlife Research Division, Environment and Climate Change Canada, Saskatoon, SK, Canada

5 Birds Canada, Port Rowan, ON, Canada

\*Corresponding author; Email: david.iles@ec.gc.ca

D.T.I. ORCID: 0000-0002-7251-4938

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**Abstract**

Inaccessibility of large portions of the boreal forest adds uncertainty to results of range-wide population assessments based on the North American Breeding Bird Survey (BBS). Systematic counting of migrants has the potential to assess population status across the entire migration route passing by a single monitoring station, making migration monitoring an attractive addition to the toolkit for boreal monitoring. Numerous bird observatories across North America have collected decades of standardized daily counts during fall and spring migration seasons with a goal of monitoring avian population dynamics; however, statistical approaches to appropriately weighting station-level trends in national-scale analyses have hitherto been elusive. Here, we describe a multi-level statistical model that estimates population trajectories within and across all portions of the breeding range by integrating migration count data from locations for which breeding ground origin of the migrants counted at each site can be broadly delineated. We applied this model to Blackpoll Warbler (*Setophaga striata*), a species of conservation concern, and compared migration-based population trend estimates to those from the BBS. Migration-based trend estimates for Blackpoll Warbler were largely consistent with those from the BBS and suggest that the Canadian national population has declined over the most recent 10 years (3 generations). Trends are strongly negative in the portion of the species’ boreal breeding range from the Great Lakes eastward, where populations have likely declined by over 30%, but stable and increasing further west. Precision of migration-based trend estimates is currently lower than from breeding season surveys but could be improved with additional data from migration monitoring stations. Application of our method to other species inadequately monitored throughout their life cycle be an important advance for North American landbird monitoring. Our approach yields independent trend estimates that can be used to validate conventional breeding surveys for which spatial biases in data collection are a major concern.

**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. 2016, 2019). 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 et al. 2014). Many boreal-breeding species migrate 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 population status in select regions of northern forest, range-wide trends of most boreal species are lacking (Dunn et al. 2005).

There has long been interest in using standardized counts of migrating birds 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 et al. 2005; Farmer et al. 2007). Counting migrants for use in population monitoring is a specific goal of The Canadian Migration Monitoring Network, a collaborative initiative of bird observatories across Canada, Birds Canada, and Environment and Climate Change Canada (Crewe et al. 2008, Dunn et al. 2021), and similar data are collected by several long-running migration monitoring stations in the United States. However, migration monitoring data have typically been analyzed on a station-by-station basis (Crewe et al. 2016, Kamm et al. 2019), due to lack of knowledge of the breeding ground origins of migrants passing count stations. This gap in knowledge precludes appropriate weighting of site-specific trends in combined analyses to derive regional or range-wide trends, while also hampering appropriate targeting of conservation action.

Advances in probabilistic origin assignments using stable hydrogen ratios in feathers, have led to cost-efficient methods for broadly determining the breeding ground origins (hereafter ‘catchment areas’) of birds captured at migration count sites (Van Wilgenburg and Hobson 2011, Hobson et al. 2015, Dunn et al. 2023). Knowledge of catchment areas provides a powerful opportunity to appropriately weight information across a network of migration monitoring stations and to 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. 2020). 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). Migration monitoring methods provide an attractive alternative method for tracking population status in boreal species, because individuals from all parts of the breeding range must pass through southern areas during migration, allowing count sites to sample birds from every part of their respective catchment areas.

Here, we develop a Bayesian integrated population model to estimate regional and national population trends using standardized daily counts of migrants from a series of monitoring stations, combined with estimates of station catchment areas 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 area, thereby moving beyond station-by-station analyses. 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 recommendations for expanding this method to other species.

**Methods**

*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 and parameter specifications underlying the statistical model are described in Tables 1 and 2. Limits for parameter values (Table 2) wee based on decades of migration counts from members of the Canadian Migration Monitoring Network.

Quantities in the model 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 . 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. In cases where a migration monitoring station is known (or assumed) to exclusively capture birds from a subset of strata, the relevant parameters ) are fixed to zero for the strata that are not monitored by the station. We note that stratum abundances in the baseline year of the model (i.e., ) are not estimable with migration data alone, because infinite combinations of and migration parameters ( would be equally consistent with the observed data. Thus, we fixe such that the model estimates change relative to the start year within each stratum, ensuring all parameters are theoretically identifiable.

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.

We use 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. The latent cell probabilities describing the multinomial distribution (i.e., ) therefore allow station-level dynamics to be linked to stratum-level dynamics.

Finally, estimates of percent population change in a stratum (indexed by *j*, Table 1) relative to a baseline year (in this study, relative to the year 2000), are calculated as:

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

where is an index of abundance in the final year (), and is an index of abundance in the baseline year (). Population trend, defined as geometric mean rates of change between two points in time to match the measure of population trend used by 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 (Table 1). 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.

*Testing the model for Blackpoll Warbler: data and model parameters*

We applied our statistical model to time series of migration counts of Blackpoll Warblers (standardized daily counts) collected from 2000-2018 at permanent monitoring locations across Canada and the United States. Canadian sites are members of the Canadian Migration Monitoring Network, which use station-specific standards to collect avian counts during the pre-breeding (‘spring’) and/or post-breeding (‘fall’) 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 at most sites is 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 fixed 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, Dunn et al. 2021). Data from U.S. bird observatories consist of daily captures with mist-nets, usually with fixed locations and operated for similar hours as at Canadian sites for least 5 days per week during spring and/or fall migrations. Because some U.S. stations had variable daily hours and/or number of nets, daily number of net-hours was used as a statistical offset in analyses.

Daily counts for Blackpoll Warbler were available for 13 monitoring sites during pre-breeding migration and 18 sites in post-breeding migration (Appendix 1). Data from each site were restricted to dates that were sampled in at least two-thirds of years in which the station operated. Within those date limits, daily samples had to have been made during at least 75% of days within local migration season for blackpolls. Specific days with <50 total net hours were omitted from analyses. For sites with notable changes in count effort between 2000 and 2018, data were limited to the years within which coverage was standardized.

We split the boreal breeding range of the Blackpoll Warbler into two geographic strata: ‘West’ and ‘East’ (Figure 1), based on feather stable hydrogen isotope analysis and other information in Dunn et al. (2023). Those authors defined three strata, but we combined the two covering all areas west of the Great Lakes into our single West stratum due to sample size considerations. Breeding ground origins of Individual blackpolls can be confidently assigned to one or the other stratum based on stable hydrogen isotope ratios in their tail feathers (Dunn et al. 2023). The boundaries of these strata are also consistent with other knowledge of Blackpoll Warbler migration routes, based on banding, geolocator, and additional stable isotope studies (DeLuca et al. 2015; Holberton et al. 2015, Morris et al. 2016; Covino et al. 2020).

With a few exceptions, we used the feather isotope results from Dunn et al. (2023) as priors in our statistical population model to indicate the proportion of migrants originating from East and/or West strata (,,,,). Stable hydrogen isotope ratios in parts of Alaska have the same values as expected in the East stratum, however, but because migrants captured far west of the Great Lakes can safely be assumed to have originated from the West stratum we fixed the West proportion at 100% without regard to isotope results. Elsewhere we assigned values based on isotope results from the nearest location within 500 km for which isotope results were available. Finally, for sites with no data for estimating West vs. East proportions of migrants, we assigned no prior The values assigned to each site in each season and the basis for each selection are shown in Appendix 1.

For an estimate of relative abundance in the East and West strata for Blackpoll Warbler, we used predictions of based on eBird (Fink et al. 2022), in which high-resolution rasters (2.96 km pixel width) describe model-derived predictions of relative abundance across North America during the breeding season). 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 East stratum than in the West We therefore re-scaled estimates of based on these values, using , where was 1.34 and 1 for the East and West, respectively.

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. Using simulation we evaluated whether the migration model was able to generate unbiased estimates of regional population trends across a wide range of regional trajectory scenarios, and tested model sensitivity to changes in fixed parameter values.

*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 et al. (2017) and Smith and Edwards (2021). To derive regional trend estimates from the BBS, we assigned BBS analytical strata into Eeast and West categories based on geographic overlap with the strata we used for migration analysis (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](about:blank) (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 (Appendix 3).

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 3; 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%; Table 3).

Pre-breeding migration and BBS both suggested that Blackpoll Warbler populations had likely occurred in eastern North America since 2000 (Table 3; 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 3), 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 4.

**Discussion**

We developed a novel statistical model to estimate regional and national population trends by using stable isotope information to empirically weight data across an international network of migration monitoring stations. Our approach provides independent trend estimates that can be compiled and compared to those from the North American Breeding Bird Survey, which primarily monitors the range margins of species inhabiting the boreal forest ( ). Evaluating potential biases in existing trend estimates for species with limited BBS coverage is a priority (Hudson et al. 2017). Our study therefore fulfills a longstanding need for North American landbird monitoring (Dunn et al. 2005) and represents an important tool for determining status of migratory species that are not well-surveyed by other methods (Hobson et al. 2015).

Applying our model to Blackpoll Warbler yielded national trend estimates that were broadly consistent to those from the BBS, indicating that both can detect signals of range-wide population change despite each survey’s limitations. In particular, national trend estimates from BBS and both fall and spring migration monitoring were similar in magnitude and direction, and all agreed that the national population likely declined from 2000 and 2018. All three surveys also indicated there was a moderately low, though non-negligible, probability that the national population has declined by more than 30% over three generations and meets the criteria for ‘Threatened’ status under the Canadian Species At Risk Act. Although the precision of trend estimates is currently lower for migration monitoring than from the BBS, we recommend that future species status assessments consider estimates from both surveys simultaneously, given that biases in breeding season surveys could change as breeding distributions shift in response to a changing climate, or if migration pathways shift over time.

We also suggest that future efforts should continue monitoring changes in migration routes, and additions through time at individual stations (e.g., through recurring collection of stable isotope data), which could be used to identify temporal biases and improve precision in migration-based trend estimates.

Unfortunately, we are unable to estimate a national 50-year migration-based trend for comparison to the long-term BBS trend. Our approach requires a network of stations to estimate national trends, and few stations collected data prior to 2000 (Appendix F). Long-term trend estimates from the BBS suggest that North American Blackpoll Warbler populations have declined by more than 95% since 1970, representing a loss of 307 million breeding adults (Data S1 in Rosenberg et al. 2019). The two migration monitoring stations that have been in operation since 1970 detected contrasting station-level trends for Blackpoll Warbler. Long Point Bird Observatory (LPBO) has detected increasing numbers of Blackpoll Warblers in both spring and fall (Figs F1 and F2 in Appendix F), while Manomet Observatory (MO) has detected a long-term decline since 1970 in both spring and fall, though this trend has reversed in recent years (Figs F3 and F4 in Appendix F). Yet, a key message of our analysis is that trends at individual monitoring stations do not necessarily reflect national or regional trends in a straightforward way. Both stations receive birds from multiple (and different) regions simultaneously, and each station-level trend reflects a complex mixture of regional trends, plus stochastic annual contributions owing to environmental effects. The contrasting long-term patterns in migrants at these two monitoring sites could suggest that different regions of the boreal forest have experienced different long-term trajectories, but we are unable to evaluate regional dynamics directly given the lack of historical stable isotope data and paucity of long-term (i.e., pre-2000) data at other migration monitoring stations. 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 .

The apparent congruence between recent trend estimates from migration monitoring and BBS is somewhat surprising, given that the BBS samples a geographically biased portion of the Blackpoll Warbler range. Ecological theorypredicts population trends will be more negative at species range margins (i.e., at BBS survey locations), where habitat quality is lower and environmental conditions are further from a species’ optimum (Hargreaves et al. 2014; MacArthur, 1984). The BBS also disproportionately samples anthropogenically disturbed boreal habitats (Van Wilgenburg et al. 2015), and recent evidence suggests that a 600 km northward shift in the Blackpoll Warbler’s eastern 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. We expect migration monitoring to be more robust to sources of bias in BBS, since monitoring stations capture birds from across the species range and populations that have shifted their breeding locations will nevertheless continue to be surveyed during their migration. Application of our method to a larger number of boreal breeding species would provide a strong test of whether BBS-derived trends are generally pessimistic for species experiencing degradation of breeding range in the southern boreal and/or 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 et al. 2007), for which BBS-derived trend estimates are highly uncertain.

*[Note sure this paragraph is really necessary]* Our analytical framework can generate regional estimates of relative population change but requires independent estimates of abundance within each analytical stratum to produce a correctly weighted national trajectory. For North American landbirds, considerable progress has been made towards understanding the relative strengths and limitations of different datasets used for this purpose (Confer et al. 2008; Sólymos et al. 2020; Thogmartin, 2010). 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 (Boreal Avian Modeling Project, 2020; Stralberg et al. 2015), 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), which can be used to test predictions from our model and generate improved model outputs.

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, although this would not be an issue for most boreal species. Simultaneously, the continual improvement of wildlife tracking technologies will undoubtedly yield finer resolution estimates of migration routes, 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.

**Authors’ Contributions**

DTI developed statistical model, led analysis, and wrote the initial draft manuscript. EHD and DE compiled and cleaned migration count data. All authors contributed throughout to ideas, discussion and editing.

**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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