An evaluation of isotopic (δ^2H) methods to provide estimates of avian breeding and natal dispersal

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Abstract.   Natal and breeding dispersal represents an important component of animal demography and metapopulation theory. This phenomenon also has implications for conservation and management because understanding movements of individuals potentially allows the identification of key habitats that may be acting as population sources or sinks. Intrinsic markers such as stable isotope abundance in tissues that can be associated with provenance can provide a coarse but pragmatic solution to understanding such movements. Different methodologies have been proposed to quantify natal and breeding dispersal by using stable isotope analyses of keratinous tissues (hair, feathers), each of them with their own advantages and limitations. Here, we compared results provided by four different methods to estimate dispersal (three already published and one novel) in animals using stable isotope measurements. We used a single large dataset of feather δ^2H values from golden-winged warblers (*Vermivora chrysoptera*) representing five different populations breeding in North America to compare model results. We propose one method as the most adequately supported by data, and we used this method to demonstrate how biological factors explaining dispersal status can be identified and geographical origins of immigrants inferred. Our results point to a generalized methodological approach to using stable isotope data to study immigration and dispersal in birds and other animals.

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INTRODUCTION

The dispersal of individuals from natal and breeding locations to sites of first or subsequent breeding represents an important component of animal demography and metapopulation theory (Greenwood and Harvey 1982, Walters 2000). This phenomenon is especially relevant to the conservation and management of long-distance migratory birds because an understanding of the movement of individuals at various scales allows for more informed decisions about the protection of key habitats. By identifying which populations are acting as sources or sinks at local, regional, and continental scales (Donovan et al. 1995a, b), focus can be placed on protecting source

populations and those regions acting as ecological traps can be identified (Holmes and Sherry 1992, Hobson et al. 2001, Webster et al. 2001). Despite recognition of the key importance that natal and breeding dispersal have on population demography, little progress has been made since the seminal review paper by Greenwood and Harvey (1982). This contrasts with significant developments in the use of miniaturized tracking devices (Bridge et al. 2011, 2013) that has allowed major advances in delineating migratory routes and connectivity between breeding and wintering grounds (Rushing et al. 2014, Hobson et al. 2015, 2016, Cohen et al. 2017). This lack of progress is understandable because of the immense challenge of marking and following enough individuals over space and time to provide meaningful inference into the frequency, scale, and biological significance of such movements. Given the challenges of studying dispersal using traditional marking techniques such as radio telemetry, data from the use of intrinsic markers such as stable isotopes (Hobson et al. 2004, Studds et al. 2012, Van Wilgenburg et al. 2012), genetic markers (Ruegg et al. 2017), and trace elements (Poesel et al. 2008) obtained from individuals sampled across numerous breeding populations can provide a coarse but pragmatic alternative. Moreover, even if precise natal or previous breeding origins are not discernable, it may still be possible within acceptable margins of error, to identify those individuals that derive from the local population vs. immigrants. The measurement of naturally occurring stable isotopes in tissues of animals provides one such intrinsic marker that can potentially be used to estimate the rates of immigration into populations, providing those immigrants derived from regions that were isotopically different from the population of interest.

The stable isotope approach is based on the fact that naturally occurring stable isotope ratios of several elements in foodwebs show systematic spatial variation and these patterns are reflected in the tissues of higher-order consumers. Such spatial patterns have been termed "isoscapes," and they form the basis of tracing movements of animals through the isotopic measurement of their tissues (West et al. 2010, Hobson and Wassenaar 2018). In particular, the continental structure of stable hydrogen isotope (δ^2H) values

in animal tissues has proven to be immensely useful due to the strong latitudinal pattern in this isotope and the clear demonstration that birds can be probabilistically placed to origin using long-term isotopic data available for most continents (Hobson and Wassenaar 2018). Other stable isotopes, such as those of carbon (δ^{13}C), nitrogen (δ^{15}N), and sulfur (δ^{34}S), are of less universal use but do show strong regional patterns that can assist in assignment (Graves et al. 2002, Hobson et al. 2012a, Haché et al. 2014, Hobson and Kardynal 2016). In North America, amount-weighted average δ^2H values in precipitation change predictably with latitude and these isotope patterns are incorporated into local food-webs and ultimately in the feathers grown by birds at those locations (Hobson et al. 2012b). Most adult songbirds in North America molt flight feathers on or near their breeding sites prior to autumn migration (Pyle 1997), whereas hatch-year (HY) birds maintain the flight feathers they grew on natal sites until their second year (SY). Therefore, the δ^2H values of flight feathers the following spring should provide information on (1) the approximate latitude of natal origin in the case of one-year-old birds, or (2) approximate previous breeding latitude in the case of older birds (Hobson et al. 2004).

The first quantitative attempt at using stable isotope measurements to infer population structure was by Hobson et al. (2004) who examined the feather δ^2H and δ^{13}C distributions across several isolated populations of ovenbird (*Seiurus aurocapilla*) and American redstart (*Setophaga ruticilla*) in southern Canada. That study primarily used the range of variation in feather isotope values to reveal outliers that could be associated with non-local breeding birds. They estimated that 0–29% of individuals were immigrants with SY individuals showing higher rates of immigration than after-second-year (ASY) individuals. Since then, a few additional studies have attempted to pursue this approach. Studds et al. (2012) used feather δ^2H values of adult breeding Bicknell's Thrush (*Catharus bicknelli*) to derive expected resident values for 25 breeding populations representing 500 individuals. Those authors then assigned origins to all unknown birds breeding for the first time (after correcting for any age effects on feather δ^2H) and derived minimum dispersal distances for individual birds.

They estimated that 59% of all first year birds sampled were dispersing immigrants to their site of first breeding with most of these dispersing <200 km from their natal sites. Van Wilgenburg et al. (2012) estimated dispersal rates of Sprague's pipit (*Anthus spragueii*), Baird's sparrow (*Ammodramus bairdii*), and savannah sparrow (*Passerculus sandwichensis*) breeding on the Great Plains of North America. Depending on the species and odds ratio, that study found that the number of immigrants ranged from 2% to 67% and adapted a probabilistic approach to the assessment of dispersal rate using odds ratios, which represent a balance between correctly categorizing either local or immigrant individuals (Wunder 2007). Haché et al. (2014) used δ^2H and $\delta^{34}S$ values of feathers of ovenbirds breeding in New Brunswick, Canada, to infer that natal dispersal rates were low and primarily involved movements within 200 km. Most recently, using an isotope approach, Rushing et al. (2015) found relatively low dispersal rate for American redstarts (15% immigrants), and they showed that the source of immigrants varied substantially across years depending on breeding phenology. In addition, Rushing et al. (2015) also found that overall natal dispersal was higher than breeding dispersal but they may occur at similar rates in some years, and that environmental conditions experienced during winter carried over to affect the source of immigrants breeding for the first time.

In this study, we obtained feathers from breeding adult golden-winged warblers (*Vermivora chrysoptera*) from five populations ranging from the Great Lakes (Minnesota and Wisconsin, USA) to the northernmost isolated breeding population (Manitoba, Canada). In several cases, we had individuals of known history as a result of local banding programs and so could confidently identify a portion of individuals as known locals (i.e., they grew feathers at the location during the previous year). However, at other sites, this was not the case. This underlines the fact that there are several methodological questions to be resolved with respect to applying stable isotope measurements of bird feathers in order to evaluate patterns of immigration and dispersal. These questions primarily pertain to the issue of which criteria should be used to assign individuals as locals vs. immigrants. Do we assume that at any given time the isotopic structure of populations will represent locals and that statistical outliers will represent immigrants? Do we use the long-term average predicted isotope values for a population at a given location to predict who is an immigrant? Are there more robust criteria that can be used in populations that have been isotopically assayed across years and where at least some longitudinal isotopic data are available for known individuals? What statistical criteria are appropriate when considering evidence for the residency status of individuals?

Here, we investigated evidence of dispersal and recruitment among populations of golden-winged warblers throughout their range as a motivating example. Our objectives were two-fold. First, we wished to evaluate methods to infer dispersal in this species specifically. However, we were primarily interested in examining approaches that can be taken using stable isotope data to more generally define the status of individuals as being a local or an immigrant, regardless of species. Our dataset provides an important opportunity to evaluate various statistical approaches to this overriding question. Specifically, we evaluated four different approaches to evaluating the probability of an individual being an immigrant. We discuss the advantages and disadvantages of these approaches and provide new information to guide this form of assignment in future studies.

METHODS

Field sites and feather collection

We captured golden-winged warblers across the breeding range from 2009 to 2010. Birds were captured using mist-nets and call playback of male songs during the breeding period, when most individuals are territorial. Upon capture, birds were banded with a USGS aluminum band for individual identification. We determined sex based on plumage color, the presence of a cloacal protuberance and/or brood patch. Birds were aged as SY vs. ASY on the basis of plumage coloration, feather wear, molt limits, and the shape of rectrices. From each captured bird, we took the first primary feather (P1) for isotopic analysis because this feather has greater probability of being grown on breeding grounds. We separated our dataset into two subsets: known-origin birds

(captured at the same site in two consecutive years; $n = 47$) and unknown-origin birds (captured once; $n = 195$). For the second capture of known-origin birds (i.e., classified as residents), we assumed that feathers were grown in the previous year at the particular sampling site. Thus, we used the second capture of known-origin birds to build a linear model(s) between feather δ^2H values (hereafter δ^2H_f) and long-term, amount-weighted, growing-season δ^2H values in precipitation (hereafter δ^2H_p) predicted for that sampling location (Bowen et al. 2005). Unknown-origin birds constituted the bulk of our feather samples to assess dispersal and were collected along a gradient from 45.66° N to 51.03° N and from 89.55° W to 100.27° W which were loosely grouped into five sampling locations: Southwestern Manitoba (mean latitude, 50.90° N; mean longitude, 99.90° W), Southeastern Manitoba (49.72° N; 96.46° W), Northern Minnesota (48.24° N; 92.72° W), Central Minnesota (46.20° N; 94.43° W), and Northern Wisconsin (45.75° N; 89.67° W). Since our objective was to assess population level dispersal, we considered a sampling location as a site with a minimum of 19 birds sampled within a maximum distance of 70 km of each other. To control for inter-annual effects in δ^2H_f values, we captured warblers in each sampling location during a single year (2009 for sampling areas in Manitoba and 2010 for sampling sites in Minnesota and Wisconsin). Values of δ^2H_f were normally distributed in Southwestern Manitoba (Shapiro–Wilk test: $W = 0.98$, $P = 0.18$), Southeastern Manitoba ($W = 0.95$, $P = 0.28$), Northern Minnesota ($W = 0.92$, $P = 0.12$), and Northern Wisconsin ($W = 0.96$, $P = 0.49$). Values of δ^2H_f from Central Minnesota had a normal-like distribution but single outliers reduced normality ($W = 0.92$, $P = 0.04$).

Stable isotope analyses

Feathers were cleaned of surface oils using a 2:1 chloroform:methanol solvent rinse and then prepared for δ^2H analysis at the Stable Isotope Laboratory of Environment Canada, Saskatoon, Canada. We determined the δ^2H value of the non-exchangeable hydrogen of feathers using the method described by Wassenaar and Hobson (2003) using two calibrated keratin hydrogen-isotope reference materials. We performed hydrogen isotopic measurements on H_2 gas derived from high-temperature (1350°C) flash pyrolysis of 350 ± 10 μg feather (distal vane) subsamples in a Eurovector elemental analyzer (Milan, Italy) coupled with an VG Isoprime mass spectrometer (Manchester, UK) using continuous-flow isotope-ratio mass spectrometry (CFIRMS). Measurement of the two keratin laboratory reference materials (CBS −197‰, KHS −54.1‰) corrected for linear instrumental drift was both accurate and precise with typical within-run ($n = 6$) mean variance of ~2‰. We report all results for non-exchangeable H expressed in the typical delta notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation standard scale.

Calibration of feather isoscape

In their analysis of origins of sparrows in grassland habitat of prairie Canada, Van Wilgenburg et al. (2012) generated year-specific precipitation isoscapes using regional values from the Global Network of Isotopes in Precipitation (GNIP; IAEA 2018) and the U.S. Network for Isotopes in Precipitation (Welker 2000). These authors found substantial inter-annual variation in δ^2H_p (in turn related to periodic drought), and so their estimated immigration rates differed when using year-specific δ^2H_p compared to long-term δ^2H_p (i.e., from 0% to 11%). However, because we aimed to encourage the repeatability of dispersal analyses among researchers, we used only models derived from the long-term GNIP database (IAEA 2018), which is publicly available. Thus, we calibrated a δ^2H_f isoscape from the growing-season δ^2H_p isoscape of Bowen et al. (2005) using Generalized Linear Models (GLM) in which δ^2H_f values of known-origin birds (see section *Field sites and feather collection*) were the dependent variable and δ^2H_p values predicted for their particular sampling locations plus sampling year (i.e., 2009 or 2010) were the independent variables. Sampling locations for known-origin birds and the underlying precipitation isoscape are presented in Fig. 1. We used bootstrap regression, fitting the same GLM 1000 times, each time taking 25 randomized subsamples of the known-origin birds. In this way, we generated 1000 calibrated δ^2H_f isoscapes for each sampling year (i.e., raster layers). Our approach

resulted in mean rescaling functions of $\delta^2H_f = -56.14$ (standard deviation [SD] = 13.23) + 0.57 (SD = 0.16) × δ^2H_p for feathers sampled in 2009 and $\delta^2H_f = -56.14$ (SD = 13.23) −9.83 (SD = 3.34) + 0.57 (SD = 0.16) × δ^2H_p for feathers sampled in 2010. Across these 1000 simulations, we extracted the average raster and the SD raster ($\sigma_{rescale}$) for each of the two sampling years.

Following Van der Zanden et al. (2014), we used this bootstrapping approach to derive a spatially explicit error raster associated with the calibrated δ^2H_f isoscape (hereafter "error surface"). We obtained this error surface from the following equation:

$$e_c = \sqrt{\sigma^2_{rescale} + \sigma^2_{individual}} \qquad (1)$$

where e_c represents the error (measured in ‰) associated with a given cell (c) of the raster surface, taking into account both variation in the parameter estimates of the rescaling functions ($\sigma^2_{rescale}$) and average value of the regression residuals ($\sigma^2_{individual}$). Both sources of error were estimated from variation between iterations of the bootstrap linear models. Thus, we effectively controlled for errors in the recalibration algorithm and individual variation within sites, developing spatially explicit estimates of error combining both sources of error (Appendix S1: Figs. S1, S2).

Geographic assignment of origins

We assigned feather samples to geographic origins using a likelihood-based spatially explicit approach (Royle and Rubenstein 2004, Van Wilgenburg and Hobson 2011, Hobson et al. 2014). We first converted the long-term growing-season δ^2H_p isoscape from Bowen et al. (2005) into a
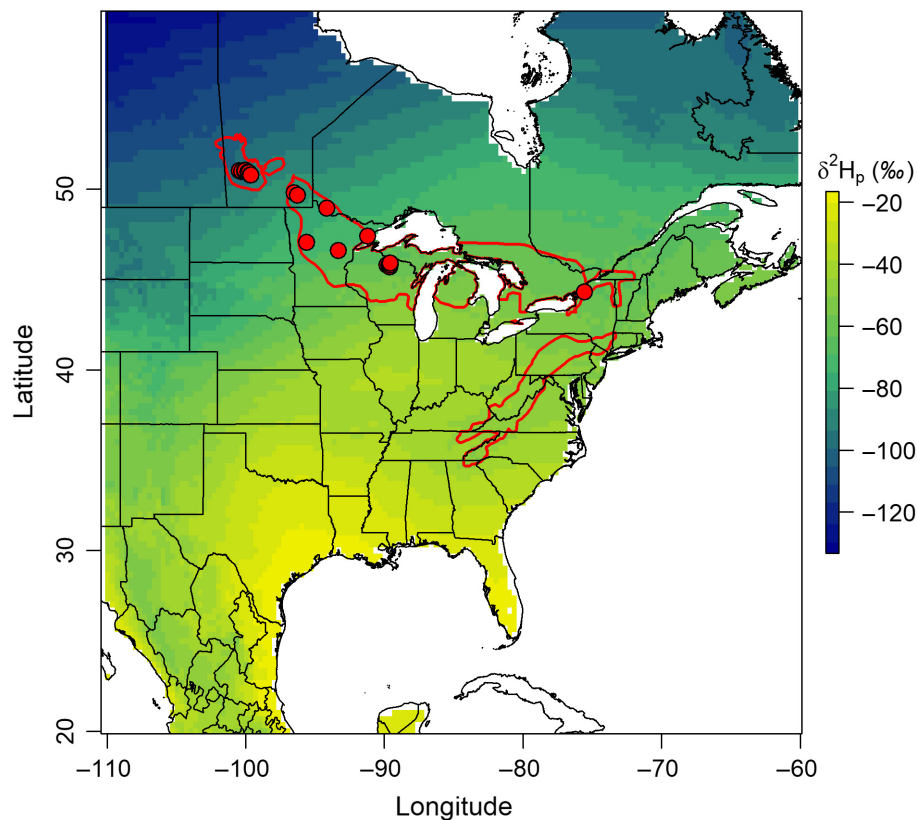

Fig. 1. Red points indicate sampling locations for known-origin birds used to calibrate the feather isoscape (n = 47). The underlying raster is the growing-season δ^2H_p isoscape (Bowen et al. 2005). Breeding range of golden-winged warbler is outlined in red.

δ^2H_f isoscape as explained above. To limit the assignment to biologically plausible origins, we clipped the calibrated δ^2H_f isoscape with the current breeding range of golden-winged warblers (Hobson et al. 2016). Subsequently, for each feather sample (i.e., individual bird) we assessed the likelihood that a given cell of the calibrated feather isoscape represented the true origin using the following normal probability density function (hereafter PDF):

$$f(y^*|\mu_c, e_c) = \left(\frac{1}{2\pi e_c^2}\right) \exp\left[-\frac{(y^* - \mu_c)^2}{2e_c^2}\right] \quad (2)$$

where $f(y^*|\mu_c, e_c)$ represents the probability that a given cell (c) is the potential origin for a sample individual (y^*), given the predicted δ^2H_f value from our calibrated isoscape for that cell (μ_c) and the predicted error (SD) for that cell (e_c).

Dispersal status

Several studies have found that δ^2H_f of nestlings and HY birds are lower compared to those of adults potentially due to differences in metabolism, diet, or feather growth phenology (reviewed by Studds et al. 2012, Haché et al. 2014). We tested this hypothesis with our data to determine whether the estimated dispersal rate could be biased by variation in δ^2H_f across age classes. Mean δ^2H_f of "SY" birds was −102.65‰ ($n = 107$), whereas mean δ^2H_f of "ASY" was −104.31‰ ($n = 78$). A linear mixed effects regression treating age as a factor and with site as a random effect showed no statistical difference between age classes ($\beta_{SY} = 1.54$, standard error [SE] = 1.01) and we consequently did not implement any age-class correction in our dispersal analyses.

We assessed the likelihood that birds were immigrants into the sampling locations where they were captured following four different methods described below (see Table 1 for comparison of methods).

Method 1: Comparison of δ^2H_f against sample of known-origin birds.—In our first method, we estimated dispersal following Rushing et al. (2015). In brief, this method is similar to conducting a z test, comparing the observed value of a feather to a normal distribution estimated from the mean and SD of a sample of known-origin individuals. We assumed that variation in δ^2H_f values of feathers grown at the same locality follows a normal distribution. Thus, we compared the observed δ^2H_f value of a given sample bird with a normal probability density function whose mean and SD were calculated from a sample of individuals from the particular sampling location. We categorized a sampled bird as either immigrant or resident into a particular sampling location, under three progressively stringent thresholds as defined by 4:1 odds, 9:1 odds, and 19:1 odds (consistent with Rushing et al. 2015). These odds ratios were used to calculate the range of δ^2H_f values representing a given area under the curve (i.e., probabilities of 0.80, 0.90, and 0.95, respectively) for each sampling location. If the δ^2H_f value of the given bird fell outside the quantiles including these cutoff probabilities, we categorized it as immigrant into the sampling location and otherwise as local (Fig. 2). Isotopic values of known-origin birds (i.e., residents) provided a reliable estimate of isotopic variation at the particular sampling location (Rushing et al. 2015). As we did not have enough known-origin birds for each sampling location, we assumed that resident birds drive the isotopic signature of each sampling site (Hobson et al. 2004). We tested this assumption at one of our sampling locations (Southwestern Manitoba) for 2009 and found no statistical difference ($F_{1, 118} = 0.17$; $P = 0.68$) in δ^2H_f of known-origin birds (mean = −109.98‰; SD = 7.10; $n = 14$) and unknown-origin birds (mean = −110.65‰; SD = 5.48‰; $n = 106$). We acknowledge that we cannot test this assumption for the rest of sampling locations because we lack data on known-origin birds, and we address this assumption in the *Discussion*.

Method 2: Comparison of δ^2H_f against local predicted value from a calibrated isoscape.—In our second method, we estimated dispersal status following Van Wilgenburg et al. (2012). This method is similar to that in Method 1, but rather than comparing δ^2H_f of the sample of interest to a normal distribution function parameterized from a sample of local individuals, it compares the δ^2H_f value against a mean prediction from a calibrated isoscape and an estimated error distribution. We assumed that variation in δ^2H_f values for feathers grown at the same locality follows a normal distribution. Consequently, we used a normal PDF to compare the observed δ^2H_f value

Table 1. Comparison of methods to assess the status of an individual as locals vs. immigrants based on analysis of $\delta^2 H$ in feathers.

Pros	Cons	Reference
Method 1. Comparison of $\delta^2 H_f$ against sample of known-origin birds		
Ease of implementation	Inference limited to sampled location(s)/population(s)	Rushing et al. (2015)
	Known-origin samples needed for each year of interest	
Method 2. Comparison of $\delta^2 H_f$ against local predicted value from a calibrated isoscape		
Potential to generalize to more locations/years	Computational complexity	Van Wilgenburg et al. (2012)
	Sampling required across gradient to calibrate isoscape	
Method 3. Distance to pixel of highest likelihood of molt origin within an isoscape		
Provides direct estimates of dispersal distance	Computational complexity	Studds et al. (2012)
Potential to generalize to more locations/years	Sampling required across gradient to calibrate isoscape	
	Competing distribution functions to select between	
Method 4. Comparison of capture location to regions of likely vs. unlikely molt origins within isoscape		
Potential to generalize to more locations/years	Computational complexity	This study
	Sampling required across gradient to calibrate isoscape	

of a given sample against the mean $\delta^2 H_f$ predicted for its capture location by our calibrated isoscape, given the expected SD of values for $\delta^2 H_f$ from our error surface (as previously defined in *Calibration of feather isoscape*). Similar to Method 1, if the $\delta^2 H_f$ value of the given sample bird fell outside the quantiles including the previous cutoff probabilities (i.e., 0.80, 0.90, and 0.95), we categorized it as an immigrant into the sampling location and otherwise was categorized as local. Since we included the sampling year as a fixed effect in the bootstrapping linear model between $\delta^2 H_f$ and $\delta^2 H_p$, we could control for inter-annual effects by associating the observed $\delta^2 H_f$ value of a given sample bird to its corresponding year-specific calibrated isoscape.

Method 3: Distance to pixel of highest likelihood of molt origin within an isoscape.—Following Studds et al. (2012), we assessed dispersal by examining the likelihood that a feather was grown in a given pixel within an isoscape. Then, we calculated distances to the highest likelihood pixel and evaluated whether this distance was an outlier given the distribution of estimated distances within the population. First, we calibrated the feather isoscape with our known-origin birds

subset, and we determined potential geographic origins of sample feathers as explained in the previous sections of this study. Since we included sampling year as a fixed effect in the bootstrapped linear model between $\delta^2 H_f$ and $\delta^2 H_p$, different rasters of feather isoscapes and probability of origins were generated for birds sampled in 2009 and 2010 (differing in the intercept value). Then, for each sampling year, we extracted the pixel that represented the highest probability of being the true origin for a feather sampled in that year (as given by Eq. 2). We then calculated the distance (in km) between the sampling location and the pixel representing the highest probability of origin for each sampled bird; if more than one pixel shared the maximum likelihood value, distance to the mean position was used. For calculating these distances, we used the Haversine formula, which determines the great-circle distance between two points assuming a spherical Earth. After pooling feathers sampled in 2009 and 2010, the distribution of calculated distances was strongly skewed because breeding site fidelity was more common than long-distance dispersal, and consequently, the most probable dispersal distances were
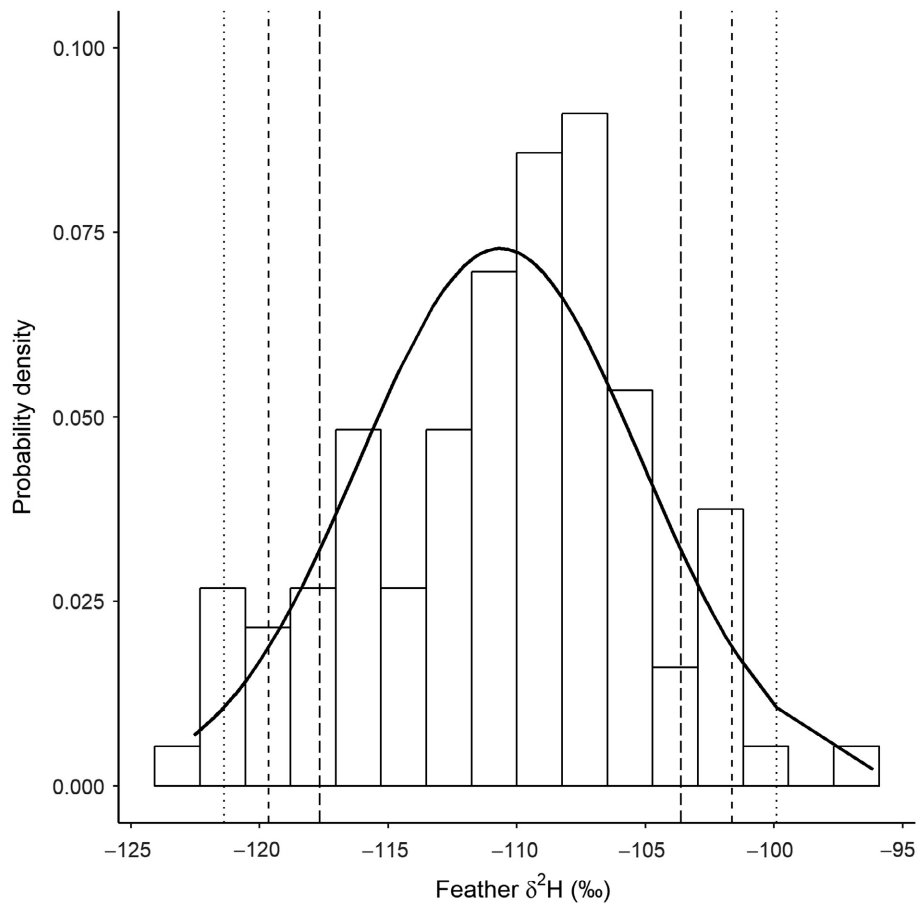
Fig. 2. Histogram of feather δ^2H values from unknown-origin birds sampled at Southwestern Manitoba ($n = 106$). The black line represents the normal probability density function fitted for feather δ^2H values of that sampling location. The different cutoffs (i.e., quantiles) excluding categorized immigrants are represented by long dashed, dashed, and dotted vertical lines, respectively, for 4:1, 9:1, and 19:1 odds ratios.

<200 km (Fig. 3). In addition, the distribution of estimated dispersal distances showed two peaks at 1100 and 1400 km, indicating that long distances are more likely to occur than medium distances. For this reason, we fit a mixed-normal PDF to the distribution of calculated distances in contrast to Studds et al. (2012) who used the exponential, Weibull and half-Cauchy distributions. We used the Expectation-Maximization algorithm to fit parametric mixture densities to our calculated distances which provides a convenient approach to approximate Markov Chain Monte Carlo samples with a parametric mixture distribution implemented with the *mixtools* (Benaglia et al. 2009) and *RBesT* packages (Weber 2018) within R (R Core Team 2017). Finally, we

extracted the quantiles that included our desired accumulated probabilities within the obtained mixed-normal PDF (i.e., 0.80, 0.90, and 0.95), and we categorized a sample bird as "immigrant" into the sampling location if its δ^2H$_f$ value fell outside these quantiles.

Method 4: Comparison of capture location to regions of likely vs. unlikely molt origins within isoscape.—In our fourth method, we estimated dispersal status using a previously unpublished methodology that assesses whether the capture location falls within the area defined as a likely molt origin for the sample. First, we used our year-specific calibrated feather isoscapes derived using our known-origin birds, and we determined the likely geographic origins of sample
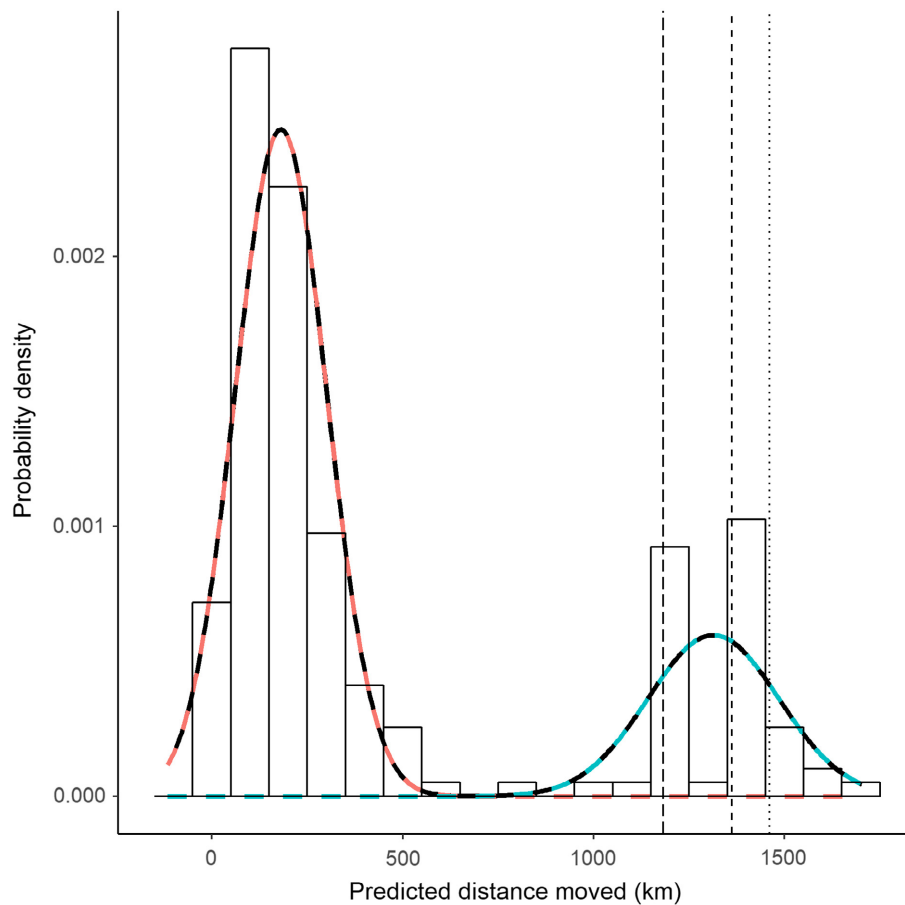
Fig. 3. Histogram of distances moved between sampling locations and predicted pixels of maximum probability of origin based on feather δ^2H analyses. Individual Gaussian density components in the mixture distribution are shown by the dashed red line (74.8% contribution), and the dashed blue line (25.2% contribution). The mixture density distribution is shown by the dashed black line. The different cutoffs (i.e., quantiles) leaving at the right side categorized immigrants are represented by long dashed, dashed, and dotted vertical line, respectively, for 4:1, 9:1, and 19:1 odds ratios.

feathers as explained in the previous sections. We then reclassified the year-specific probability of origin maps into likely vs. unlikely origins by determining the odds that any given assigned origin was correct relative to the odds it was incorrect. Based on 4:1 odds (consistent with 80% cutoffs in Methods 1–3 above) that a given assigned bird had truly originated from within that range, we coded the set of cells that defined the upper 80% of estimated probabilities of origin as 1 and all others as 0. We repeated this process for 9:1 and 19:1 odds, resulting, respectively, in raster layers with increasing number of pixels coded as 1 (respectively, the upper 90% and 95%

of estimated probabilities of origin). Finally, if a given sampled bird was captured in a pixel coded as 1, it was categorized as a local bird from that sampling location, and otherwise, it was considered an immigrant.

Comparison of methods to assess dispersal status

For Methods (1–4) used to assess dispersal, we used a Chi-squared (χ^2) test to determine whether the number of birds categorized as immigrants differed from that expected by chance alone given the specific odds ratio. In other words, if we found a significant χ^2 value for this test, the proportion of immigrants

categorized would be significantly different from proportions expected to be correctly classified to their origins given the associated odds ratios (i.e., 0.80, 0.90, and 0.95). On the other hand, if we found a non-significant χ^2 value, the number of birds assessed as being immigrants would only reflect the number expected due to assignment error and thus would not provide any biologically meaningful assessment of the proportion of immigrants into the population. Depending on the methodology, the categorization of a given bird as immigrant was done either for each specific sampling location (i.e., Method 1), each sampling year (Methods 2 and 4), or for all pooled data (Method 3). Therefore, Chi-squared (χ^2) tests were conducted across different data subsets accordingly.

Since known-origin birds are resident by definition, we tested our four described procedures to assess dispersal with this data subset ($n = 47$) and we quantified the error rate under each odds ratio as simply the proportion of known-origin birds being categorized as immigrant. Sample size of known-origin birds differed strongly among sampling locations; therefore, we only had two sampling locations (Southwestern Manitoba and Northern Wisconsin) for which we could test the error rate of dispersal status assessed by the method of Rushing et al. (2015).

Finally, we selected which of the four methods described above was the most adequately supported by the data based on both the Chisquared (χ^2) test and the estimated error rate.

Biological variables explaining dispersal status

We tested which biological variables determined dispersal status within a sampling location. For this purpose, we used the categorization of immigrant (i.e., one) vs. resident (i.e., zero) obtained from the best supported method as the dependent variable in subsequent analyses. We used GLM to test if the probability of a given bird being immigrant into a sampling location was related to age class (SY vs. ASY), distance to edge of the breeding range, and to local population trend as estimated from the North American Breeding Bird Survey (Sauer et al. 2014). We did not test for sex-biased dispersal owing to a lack of samples from females. We used a binomial error distribution and the complementary log-log link function (cloglog)

because of the high number of zeros in the response variable (Zuur et al. 2009). We constructed eight competing a priori models and we chose the most parsimonious ones based on $\Delta AIC_c < 6.0$ (Burnham and Anderson 2002, Richards 2008). The confidence intervals for predictor variables (hereafter 85% CI) were calculated using the parameter estimates and associated SEs. We assumed that a predictor significantly contributed to explain the response variable when the 85% CI for the estimated parameter excluded zero (Arnold 2010).

We suspected that SY birds would have a higher probability of being immigrant vs. ASY birds, as has been previously found (Greenwood and Harvey 1982, Hobson et al. 2004, Rushing et al. 2015). We also considered those populations showing BBS declines or increases to be more likely to experience an influx of immigrants compared to stable populations. It is possible that declining populations might be supported via immigration, or that immigrants may be attracted to increasing populations due to habitat quality and conspecific attraction or just that populations increases are a direct result of immigration. But we acknowledge that such predictions are impossible without knowing the source–sink dynamics of the metapopulation (Donovan et al. 1995*a, b*). Finally, we included distance to range edge as a covariate since the central–marginal hypothesis predicts that individuals should move from large central populations that produce excess individuals to peripheral populations if dispersal is random (Eckert et al. 2008) in addition to the species' range edge limiting the number of directions from which immigrants can originate (Schwartz et al. 2003).

All analyses were run in R version 3.3.3. (R Core Team 2017) using the libraries raster (Hijmans 2016*a*), maps (Becker and Wilks 2016), maptools (Bivand and Lewin-Koh 2017), geosphere (Hijmans 2016*b*), rgeos (Bivand and Rundel 2017), and AICcmodavg (Mazerolle 2017). Data and R scripts are provided as Supporting Information (Data S1).

RESULTS

Dispersal status

The proportion of warblers categorized as immigrants differed considerably (0–96%) depending

on the sampling location, the method to assess dispersal, and the odds ratio used (Table 2). The proportion of immigrants obtained by Method 1 was similar across the different sampling locations and Chi-squared (χ^2) tests determined that these proportions were imposed by the odds ratios we used (Table 3). For instance, the proportion of immigrants obtained by Method 1 across the different sampling locations usually ranged from 21% to 26% under a threshold defined as 4:1 odds, similar to the proportion that we would have obtained by chance alone (i.e., probability of 20% to be immigrant). By contrast, the proportion of immigrants obtained by the other methods differed across sampling locations, with the proportion of immigrants gradually increasing from north to south. Thus, at 4:1 odds ratio, sampling locations in Manitoba showed a low proportion of immigrants (from 0% to 13%), Northern Minnesota showed an intermediate proportion of immigrants (from 11% to 32%), whereas sampling locations in Central Minnesota and Northern Wisconsin showed high proportions of immigrants (from 31% to 96%). The Chi-squared

(χ^2) test also revealed that the proportion of immigrants categorized by Method 3 was determined by the odds ratio used (Table 3); however, results from this method were consistent with the latitudinal gradient in the proportion of birds classified as immigrants. This was because once we had estimated the distances between pixels of maximum probability of origin and current sampling locations in Method 3, we categorized immigrant vs. resident birds by pooling together feathers sampled in 2009 and 2010. We believe that this was the most correct approach to apply to Method 3 since the inter-annual effects on δ^2H_f values were already controlled for in the estimation of distances between pixels of maximum probability of origin and current sampling locations. Thus, there was no need to categorize immigrants separately for birds sampled in either year. In contrast, the categorization of immigrants in Methods 2 and 4 was based on the year-specific raster isoscapes, and thus, Chi-squared (χ^2) tests were conducted separately for birds sampled in different years. The proportion of immigrants obtained by Method 2 did not differ

Table 2. Number and proportion (%) of immigrants obtained across sampling locations by each method to assess dispersal (i.e., M1–4) and specific odds ratio (i.e., 4:1, 9:1, and 19:1).

Mean δ^2H_f	SD δ^2H_f	N	Odds ratio	Number of immigrants (%)			
				M1	M2	M3	M4
S-W Manitoba (2009)							
−110.64	5.48	106	4:1	24 (23)	14 (13)	0 (0)	5 (5)
			9:1	11 (10)	7 (7)	0 (0)	1 (1)
			19:1	6 (6)	2 (2)	0 (0)	1 (1)
S-E Manitoba (2009)							
−105.14	3.68	23	4:1	6 (26)	0 (0)	0 (0)	0 (0)
			9:1	1 (4)	0 (0)	0 (0)	0 (0)
			19:1	0 (0)	0 (0)	0 (0)	0 (0)
Northern Minnesota (2010)							
−107.76	10.94	19	4:1	2 (11)	6 (32)	2 (11)	6 (32)
			9:1	2 (11)	5 (26)	2 (11)	6 (32)
			19:1	1 (5)	4 (21)	2 (11)	4 (21)
Central Minnesota (2010)							
−85.67	7.64	28	4:1	6 (21)	25 (89)	27 (96)	27 (96)
			9:1	1 (3)	25 (89)	26 (92)	27 (96)
			19:1	1 (3)	22 (79)	4 (14)	25 (89)
Northern Wisconsin (2010)							
−81.92	6.45	19	4:1	5 (26)	16 (84)	6 (31)	15 (79)
			9:1	2 (10)	15 (79)	0 (0)	12 (63)
			19:1	2 (10)	15 (79)	0 (0)	4 (21)
Total		195	4:1	43 (22)	61 (31)	35 (18)	53 (27)
			9:1	17 (9)	52 (27)	28 (14)	46 (24)
			19:1	10 (5)	43 (22)	6 (3)	34 (17)

Note: SD, standard deviation.

from that expected by chance alone when using 9:1 and 19:1 odds ratios for the subset of feathers collected in 2009 (Table 3). Regarding Method 4, Chi-squared (χ^2) tests were always significant, and therefore, the proportion of immigrants categorized by this method was not imposed by the specific odds ratio used (Table 3).

Consistent with the compromise between spatial precision and assignment accuracy of the different odds ratios, the proportion of birds categorized as immigrants usually decreased when shifting from 4:1 odds to 19:1 odds, and the rate of misclassification (for known-origin individuals) decreased as well (Table 4). The estimated error rate ranged from 0% to 20% across different methods and odds ratios, with the lowest error rate achieved using Method 4 (from 0% to 15%). Therefore, based both on the Chi-squared (χ^2) tests and on the estimated error rates, Method 4 was the most adequately supported by the data.

Biological variables explaining dispersal status

Based on our previous results, we examined factors associated with golden-winged warblers being categorized as immigrants vs. residents as determined from Method 4 (above). We ran our candidate models across the three different odds ratios, and because results did not change, we only present results here based on a 4:1 odds ratio. Since our dataset was strongly biased toward males, we repeated our candidate models excluding females, but ultimately we pooled data from both sexes to increase sample size because the results were virtually unchanged.

Based on a cutoff criterion of $\Delta AIC_c < 6.0$, our top model set included three different candidate models. The most parsimonious model included population trend and age class (Appendix S1: Table S1). Both variables had parameter estimates with 85% CIs excluding zero (Appendix S1: Table S2). Interestingly, the lower the local population trend, the higher the probability a given warbler would be an immigrant in a particular sampling location (Fig. 4). In addition, SY birds were between 1.3 and 2 times (for rates of population change of −5 and 20% per yr, respectively) more likely to be an immigrant into a local population than ASY birds (Fig. 4). The second-best competing model included population trend, age class, and their interaction term (Appendix S1:

Table S1). Again, 85% CI of the effects of population trend and age class on dispersal status excluded zero, but 85% CI of the effects of their interaction term included zero (Appendix S1: Table S2). Finally, the third model included only population trend and 85% CI of its parameter estimate excluded zero (Appendix S1: Tables S1, S2).

We further investigated the nature of dispersal assigning individuals categorized as immigrants by Method 4 to the aforementioned isoscape. For each sampling location, birds categorized as immigrants into the local population were generally assigned to origins southeast of the breeding location (Fig. 5).

Discussion

Using δ^2H analyses of feathers to derive approximate natal and molt origins of birds has become an established tool on several continents (Hobson and Wassenaar 2018). Fewer studies have attempted to use this approach to understand dispersal and specifically to ascertain the probability of any individual being a local or immigrant into a breeding population. As we have shown, establishing dispersal rates is not straightforward and the choice of assignment approach can strongly influence the outcome of such investigations. We identified three primary approaches (Methods 2–4) that can be implemented at the individual level, providing a simple way to control for inter-annual effects in precipitation δ^2H values, and also providing a spatially explicit quantification of the error associated with the geographical assignment of origins. In addition, these methods can be applied using different odds ratios, and thus, researchers can choose the level of error to be assumed in the categorization of immigrant vs. resident birds.

Method 1, based on the methodology of Rushing et al. (2015), was the least reliable in our case. This approach requires the number of birds sampled in a given year and sampling location to be sufficient to build location- and year-specific normal probability density functions for δ^2H_f values. In our case, we needed a minimum of 19 birds captured within the same sampling year and location. This fact will undoubtedly influence sample sizes used to assess dispersal to only those breeding populations for which sampling effort is high, thus often limiting the geographic scale of

Table 3. Results from Chi-squared (χ^2) tests to determine whether the number of birds categorized as immigrants differed from that number expected from chance alone given the specific odds ratio.

Data subset	Odds ratio	χ^2 (P)
Method 1		
S-W Manitoba	4:1	0.46 (0.54)
	9:1	0.02 (1.00)
	19:1	0.10 (0.82)
S-E Manitoba	4:1	0.53 (0.61)
	9:1	0.82 (0.51)
	19:1	1.21 (0.41)
Northern Minnesota	4:1	1.07 (0.40)
	9:1	0.00 (1.00)
	19:1	0.00 (1.00)
Central Minnesota	4:1	0.03 (1.00)
	9:1	1.29 (0.36)
	19:1	0.12 (1.00)
Northern Wisconsin	4:1	0.47 (0.56)
	9:1	0.00 (1.00)
	19:1	1.22 (0.24)
Method 2		
2009	4:1	6.75 (<0.01)
	9:1	3.00 (0.10)
	19:1	3.23 (0.11)
2010	4:1	108.19 (<0.01)
	9:1	248.24 (<0.01)
	19:1	453.36 (<0.01)
Method 3		
All pooled	4:1	0.51 (0.52)
	9:1	4.12 (0.05)
	19:1	1.52 (0.25)
Method 4		
2009	4:1	20.96 (<0.01)
	9:1	12.197 (<0.01)
	19:1	4.85 (0.04)
2010	4:1	114.68 (<0.01)
	9:1	248.24 (<0.01)
	19:1	281.37 (<0.01)

Notes: Data subset used for these tests was different across procedures to assess dispersal (see *Methods* for details). Presented *P*-values have been estimated by Monte Carlo simulation (based on 10,000 replicates).

Table 4. Number and proportion (%) of known-origin birds mis-classified as immigrants in each method to assess dispersal and specific odds ratio.

Odds ratio	Number of immigrants (%)
Method 1 (S-W Manitoba)	
4:1	5 (17)
9:1	3 (10)
19:1	2 (7)
Method 1 (Northern Wisconsin)	
4:1	1 (13)
9:1	1 (13)
19:1	0 (0)
Method 2	
4:1	9 (20)
9:1	4 (9)
19:1	2 (4)
Method 3	
4:1	7 (15)
9:1	5 (11)
19:1	2 (4)
Method 4	
4:1	7 (15)
9:1	2 (4)
19:1	0 (0)

Note: Data subset was known-origin birds ($n = 47$), except for Method 1, which was 30 and 8, respectively, for Southwestern Manitoba and Northern Wisconsin.

inference to a few populations. This prevented us from assessing dispersal rates of golden-winged warblers breeding in the Appalachians because our sample size was relatively low and scattered there. By contrast, using either of the other methodologies we describe, even single birds sampled within a given locality can be categorized as local or immigrant into that sampling location. By applying a Chi-squared test, we revealed that the number of birds classed as immigrants did not differ from the number expected from chance alone when using Method 1 to assess dispersal (as well as when using Method 3). Thus, the proportion of immigrants obtained for each sampling location using Method 1 (Table 2) was similar to the proportion given by the odds ratios (Table 2; 20% with odds ratio 4:1) and so was not necessarily biologically meaningful. Nevertheless, Method 1 can still be useful when study sites have been extensively monitored and when the hypotheses addressed are not related to the proportion of immigrants itself but to the origin of these immigrants (Rushing et al. 2015).

In contrast to the other methods, Method 4 provided estimates of dispersal that were not biased by the selected odds ratio, and this method also had the lowest rates of classification error for known-origin individuals. Given the lower rates of classification error and flexibility of this approach, we suggest that Method 4 provides the most generally useful approach for examining dispersal at large spatial scales such as those involving range-wide origins. Here, we
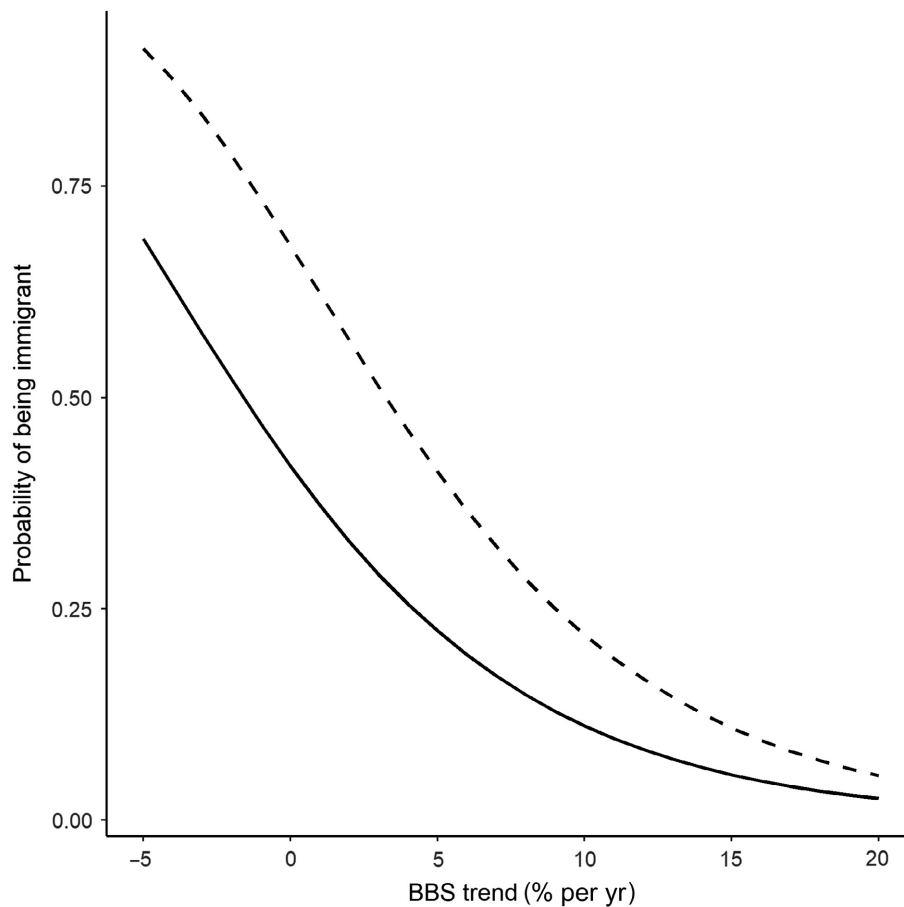
Fig. 4. Predicted probability of a given golden-winged warbler being an immigrant given the local long-term (1966–2012) population trend. Lines represent predicted values for after-second-year birds (straight line) and for second-year birds (dashed line). Parameter estimates from our most parsimonious model were used to calculate these predicted values. Population trend estimates were derived from the North American Breeding Bird Survey (BBS; Sauer et al. 2014).

demonstrated the value of Method 4 using golden-winged warbler as an example. Golden-winged warbler populations have experienced an annual decline of ~ 2.3% per yr (95% CI: −3.1, −1.5% per yr) range-wide between 1966 and 2015, with populations generally increasing or stable along the northern range edge and declining elsewhere (Sauer et al. 2017). The reasons for these declines are related to the loss of early successional habitats they prefer (Moulton et al. 2017), competition and genetic introgression with blue-winged warbler (*Vermivora cyanoptera*; Vallender et al. 2009, Moulton et al. 2017), and also to land-use changes occurring at tropical wintering areas (Kramer et al. 2017). Where

blue-winged warbler range expansion has led to sympatry, golden-winged warbler populations have generally become extirpated (Gill 1997; but see Confer et al. 2010). Thus, further understanding of immigration/emigration rates could inform both conservation efforts and our understanding of gene flow in hybrid zones. We found that the proportion of immigrants into local golden-winged warbler populations generally increased from north to south. Further analyses revealed that the probability of being an immigrant into the local population was negatively related to the local BBS population trend. Furthermore, immigrants were generally assigned molt origins south or southeast of the breeding population into
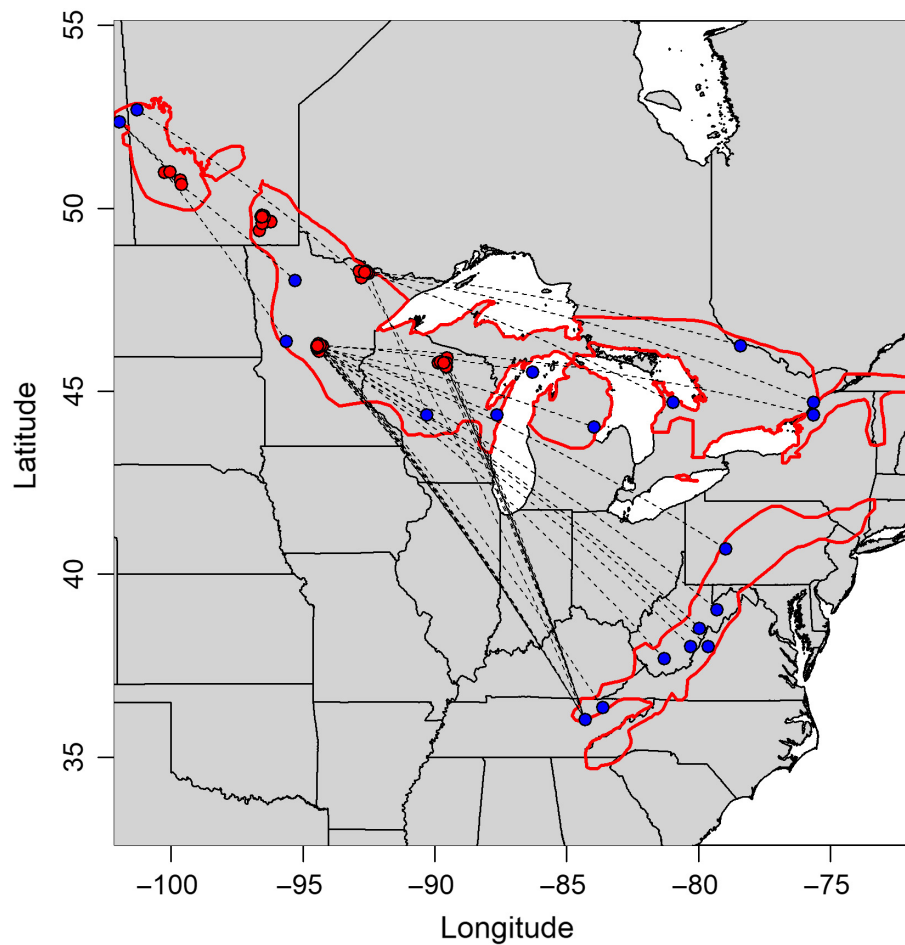
Fig. 5. Assigned geographical origin of immigrants classified by Method 4 under 4:1 odds ratio. Red points indicate our study sampling locations. Blue points indicate pixels of maximum probability of being the true origins, according to the normal probability density function used to infer geographic origins. Dashed lines indicate great-circle distances among the current sampling location (i.e., red points) and the inferred previous location (i.e., blue points). The breeding range of golden-winged warblers is outlined in red.

which they settled. These results suggest that declining populations are being supplemented by immigrants, whereas stable or increasing populations (largely in the north) are primarily made up of resident birds, supporting the occurrence of source–sink population dynamics. Although our isotope data indicate that the proportion of immigrants within a given population increases from North to South, gene flow appears to be directional from south to north, consistent with the predicted distribution shifts from climate models for this species (Crawford et al. 2016, *unpublished data*), and the known range contraction along the equatorward edge of this species range (Coristine

and Kerr 2015). Our data suggest that individuals fledging in the southernmost portions of the species range, where population declines are the steepest, are dispersing northward to mid-latitudes of the range (Minnesota and Wisconsin) and settling (Fig. 5). However, further isotopic investigations are needed especially in the southern (declining) portion of the breeding range in order to contrast patterns of gene flow with sources of immigrants. Southern golden-winged warbler populations have higher levels of genetic introgression with the blue-winged warbler (Vallender et al. 2009) and so understanding movements of individuals and genes would be fruitful.

We acknowledge that the stable isotope assignment approach using δ^2H_f in North America favors the detection of N–S dispersal movements of individuals due to the strong latitudinal gradient in δ^2H_p. Under climate change predictions, the northward movement of species may be favored (Virkkala et al. 2008, Coristine and Kerr 2015). However, future studies that are able to incorporate tracers of longitude (e.g., genetic markers, Ruegg et al. 2017) in a multi-variate assignment within a Bayesian framework (Hobson et al. 2014) could be used in conjunction with the methods employed in this study.

Previous studies have raised concern about using either long-term average or year- and site-specific δ^2H_p isoscapes in the geographical assignment of origins. In the drought-influenced American Great Plains, Van Wilgenburg et al. (2012) found substantial inter-annual variation in δ^2H_p and their estimated immigration rates of several species differed slightly when using year-specific compared to long-term δ^2H_p isoscapes. Inter-annual variation in precipitation values may be dramatic in that region and that is why these authors corrected the GNIP dataset with year- and site-specific additional δ^2H_p data. Nevertheless, other studies conducted at larger spatial scales have concluded that year- and site-specific δ^2H_p isoscapes did not improve accuracy or precision of geographical assignment of origins (Van der Zanden et al. 2014, Tonra et al. 2015). So, to encourage the repeatability of dispersal assessments based on stable isotope analyses, we recommend using assignments to the long-term growing-season δ^2H_p isoscapes provided by GNIP database (IAEA 2018) such as those created by Bowen et al. (2005). Additionally, the inter-annual effects in δ^2H_p values can be accounted for with an easier approach, as we demonstrated in this study (e.g., by including sampling year as a fixed effect in the calibration equation and propagating errors in the parameter estimates). Where there is support within the data for inter-annual variation, incorporation of year effects should provide more precise assessments and should have comparable or improved accuracy as long as parameter uncertainties are appropriately propagated.

Methods 3 and 4 provide estimates of dispersal based on the geographical assignment of a sample feather to the most-probable origin where it was grown. In this study, we used a single isotope in the probability density function to assign geographical origins, but multi-isotope approaches could also be adopted to further refine the precision of the assignment (Hobson et al. 2014) and thus the estimates of dispersal (Haché et al. 2014). This could be especially useful for other regions of the world (e.g., Africa) where δ^2H_p patterns do not follow strong latitudinal gradients such as those seen in North America but where other isotopes have proven useful (Hobson et al. 2014). In addition, because the probability density functions to assign geographical origins can be combined with any other prior information according to Bayes' Rule, the estimates of dispersal given by Methods 3 and 4 can be further refined by incorporating prior information from abundance data (Royle and Rubenstein 2004, Rushing et al. 2017), band recoveries (Van Wilgenburg and Hobson 2011, Gunnarsson et al. 2012), or genetic markers (Chabot et al. 2012, Ruegg et al. 2017). Therefore, there is a wide range of possibilities to refine these methodologies that are not yet broadly implemented.

We compared the results obtained across the four methodologies to assess dispersal using two approaches. First, we used Chi-squared (χ^2) test to determine whether the number of birds categorized as immigrants differed from that expected by chance alone given the specific odds ratio. Chabot et al. (2012) previously used this test for similar purposes and, in our case, it effectively indicated when the proportion of sample birds categorized as immigrants was close to that expected given each odds ratio. Proportion of immigrants categorized using Method 1 were not consistent with the other methods used to assess dispersal, or with the previous studies on predicted distribution shifts from climate models (Crawford et al. 2016, *unpublished data*) or genetic introgression with the blue-winged warbler (Vallender et al. 2009). Consequently, we encourage the use of Chi-squared (χ^2) test when assessing dispersal status under different odds ratios. Second, we used our subset of known-origin birds to validate methods assessing dispersal. In this way, we could quantify the misclassification rate inherent for each method and odds ratio. We acknowledge that our known-origin birds subset was used at the same time to calibrate the δ^2H_p isoscape and to validate the methods, and this

could lead to a bias in the absolute rate of misclassification. However, any possible bias should have been constant across the four methods used to assess dispersal, and our bootstrapping approach to calibrate the $\delta^2 H_p$ isoscape with 1000 randomized subsamples taken from the known-origin birds provided a robust estimate of error. Thus, we encourage the use of known-origin birds to externally validate methods to assess dispersal, particularly if sufficient samples are available to allow samples to be withheld for that purpose.

Our results point to several general recommendations that should be broadly applicable when using intrinsic markers to study dispersal. Analysts should begin by assessing whether they need to assess whether an individual is a local or immigrant into only a single or a few discrete populations or whether they need inference at large (e.g., range-wide) spatial scales. If inference is only needed for a few discrete locations, then Method 1 (Rushing et al. 2015) provides a tractable approach. However, if the ecological question needs to be assessed at large spatial scales such as in our example, then approaches using assignment of individuals to isoscapes provide a flexible approach that should be applicable to most situations. We recommend that future studies consider applying Methods 2–4 using isoscape calibration approaches similar to those used in Van der Zanden et al. (2014). Spatially explicit errors will exert a strong influence on rates of misclassification. Of the methods we considered, Method 4 seems most likely to provide accurate and precise estimates of dispersal and we suggest this method be employed in future large geographic-scale studies. Furthermore, if future studies consider alternative methods (Methods 1–4, or similar approaches), we suggest that examination of misclassification rates (using known-origin individuals) and χ^2 tests as done here provide good metrics for determining which method may be most appropriate for the data used. Finally, the importance of spatially and temporally appropriate sampling of known-origin individuals to calibrate and/or validate the assignment model cannot be over-emphasized (Wunder 2010) and thus should be a key consideration before initiating any study of dispersal employing intrinsic markers.

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