Ecological Applications, 24(3), 2014, pp. 445–456

Assessing migratory connectivity for a long-distance migratory bird using multiple intrinsic markers

Clark S. Rushing,[1,2,4] Thomas B. Ryder,[2] James F. Saracco,[3] and Peter P. Marra[2]

[1]*Program in Behavior, Ecology, Evolution, and Systematics, University of Maryland, College Park, Maryland 20742 USA*
[2]*Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, P.O. Box 37012-MRC 5503, Washington, D.C. 20008 USA*
[3]*The Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, California 94956 USA*

Abstract. Patterns of migratory connectivity are a vital yet poorly understood component of the ecology and evolution of migratory birds. Our ability to accurately characterize patterns of migratory connectivity is often limited by the spatial resolution of the data, but recent advances in probabilistic assignment approaches have begun pairing stable isotopes with other sources of data (e.g., genetic and mark–recapture) to improve the accuracy and precision of inferences based on a single marker. Here, we combine stable isotopes and geographic variation in morphology (wing length) to probabilistically assign Wood Thrush (*Hylocichla mustilena*) captured on the wintering grounds to breeding locations. In addition, we use known-origin samples to validate our model and assess potentially important impacts of isotopic and morphological covariates (age, sex, and breeding location). Our results show that despite relatively high levels of mixing across their breeding and nonbreeding ranges, moderate levels of migratory connectivity exist along an east–west gradient. In addition, combining stable isotopes with geographic variation in wing length improved the precision of breeding assignments by 10% and 37% compared to assignments based on isotopes alone or wing length alone, respectively. These results demonstrate that geographical variation in morphological traits can greatly improve estimates of migratory connectivity when combined with other intrinsic markers (e.g., stable isotopes or genetic data). The wealth of morphological data available from museum specimens across the world represents a tremendously valuable, but largely untapped, resource that is widely applicable for quantifying patterns of migratory connectivity.

Key words: deuterium; geographical variation; hydrogen isoscapes; Hylocichla mustilena; *intrinsic markers; migratory connectivity; morphology; probabilistic assignment; stable isotopes; Wood Thrush.*

INTRODUCTION

Quantifying the migratory connectivity of animal populations is essential for understanding the evolutionary processes that shape life history and the ecological processes that affect population dynamics (Webster et al. 2002), as well as for interpreting population trends (Runge and Marra 2005, Dunn et al. 2006) and determining the principal threats driving regional population trends (Hobson 2005, Faaborg et al. 2010, Marra et al. 2011). This is in large part because events in the avian annual cycle are often inextricably linked, such that events in one season can "carry over" to subsequent seasons, having profound impacts on population dynamics (Marra et al. 1998). Despite the long-standing interest in movement ecology, establishing the linkages between populations of migratory species has remained challenging because these species generally occupy a variety of disparate locations and move across jurisdictional boundaries throughout their annual cycle (Rubenstein and Hobson 2004, Webster and Marra 2005, Faaborg et al. 2010).

To track the migratory movements of birds, scientists have utilized both extrinsic (e.g., mark–recapture, VHF and satellite telemetry, light-level archival geolocators; Combreau et al. 2011, Ryder et al. 2011) and intrinsic approaches (e.g., morphology, genetics, and stable isotopes; Rubenstein and Hobson 2004). Extrinsic approaches such as mark–recapture are often limited by low recapture rates (Webster et al. 2002), whereas direct-tracking technologies can be costly (e.g., satellite telemetry) and suffer from low resolution (e.g., geolocators). Genetic markers suffer from low resolution because many migratory species show little genetic structure across their breeding or nonbreeding ranges (Colbeck et al. 2008, Irwin et al. 2011), although these markers have proven useful when such structure exists (Chabot et al. 2012, Rundel et al. 2013). Stable isotopes, however, are a valuable tool for understanding migratory patterns because, despite low resolution, they are

---

Manuscript received 10 June 2013; revised 9 August 2013; accepted 19 August 2013; final version received 10 September 2013. Corresponding Editor: T. Simons.

[4] Present address: Department of Biology, Biology-Psychology Building, University of Maryland, College Park, Maryland 20742. E-mail: crushing@umd.edu

relatively inexpensive, large numbers of samples can be obtained, and the abundance of certain stable isotopes varies predictably over large geographic areas (Hobson 2005, Hobson and Wassenaar 2008, Inger and Bearhop 2008).

In particular, stable hydrogen isotopes have emerged as a key tool for estimating migratory connectivity in many bird species. The composition of stable hydrogen isotopes in rainfall varies with latitude and altitude across North America (Bowen et al. 2005), and this stable isotopic signature is incorporated into the tissues grown at a given location (e.g., feathers and claws; Hobson and Wassenaar 1997). Because most migratory songbirds molt their feathers on their breeding grounds prior to fall migration (Pyle 1997), and because feathers are metabolically inert after growth (Hobson and Wassenaar 1997), stable hydrogen isotope signatures in feathers (δ^2H_f) can be compared with known isoscapes to determine the geographic origin of birds sampled away from their breeding sites (Hobson et al. 2012). The ability to use these feather isoscapes to make probabilistic assignments to their region of origin has been one of the largest advances for quantifying the migratory connectivity of both Nearctic–Neotropical migrants (Hobson et al. 2004, Norris et al. 2006, Sarasola et al. 2008) and Palearctic–Afrotropical migrants (Pain et al. 2004, Szép et al. 2009). Despite these advances, a number of limitations and challenges associated with using stable isotopes to make geographic assignments still exist (Van Wilgenburg and Hobson 2011).

The main limitation of using hydrogen isotopes to make probabilistic assignments and assess migratory connectivity is the limited resolution of inference. First, the continental isoscape for hydrogen isotopes provides broad latitudinal clines, but has much poorer longitudinal resolution (Bowen et al. 2005), often resulting in broad geographic assignments of origin (Wunder et al. 2005). Moreover, the precipitation-based hydrological models used to estimate hydrogen isoscapes are based on long-term averages and may fail to reflect interannual variation (Hobson et al. 2012). Second, interindividual variation due to age can reduce the resolution of assignments and decrease the probability of correct assignments (Langin et al. 2007, Haché et al. 2012). Finally, given that a number of ecophysiological factors may influence the isotopic discrimination linking rainfall and tissue, researchers may require species-specific tissue base maps and assignment algorithms (Hobson 2011, Hobson et al. 2012, Hallworth et al. 2013).

Given the challenges of using stable isotopes to quantify migratory connectivity, researchers continue to seek approaches that will improve accuracy and precision of the geographic assignments based on hydrogen isotopes. One recent advance has been the development of assignment algorithms that can probabilistically determine the origin of individuals across a continuous surface (Van Wilgenburg and Hobson 2011). Unlike earlier methods that assigned individuals to large, predefined regions (Royle and Rubenstein 2004, Boulet et al. 2006, Norris et al. 2006), the use of a continuous surface provides a more accurate assessment of potential breeding origins. Furthermore, this approach allows researchers to easily estimate the uncertainty associated with assignments by quantifying the size of the geographic area identified as potential origin (Chabot et al. 2012). The ability to quantify uncertainty is an important advance because imprecise assignments are of little use for assessing migratory connectivity even if accuracy is high (Martin et al. 2007).

A second recent development toward improving assignments and establishing linkages between breeding and wintering populations involves combining stable isotopes with other sources of data. At present, most assignments based on multiple data sources have combined multiple stable isotopes (Royle and Rubenstein 2004, Hobson et al. 2009) or stable isotope data with genetic data (Clegg et al. 2003, Kelly et al. 2005, Boulet et al. 2006, Chabot et al. 2012, Rundel et al. 2013), banding data (Van Wilgenburg and Hobson 2011), or regional abundance (Royle and Rubenstein 2004, Norris et al. 2006). Combining multiple sources of data has been shown to improve both the accuracy (Royle and Rubenstein 2004, Kelly et al. 2005, Rundel et al. 2013) and precision (Van Wilgenburg and Hobson 2011, Chabot et al. 2012) of assignments, but each of these data sources has inherent limitations and not all sources are equally useful for all species. As a result, there is a continued need to identify and combine novel data sources that can help to characterize species-specific geographical variation.

One source of geographic variation that has not been combined with stable isotopes or widely used in migratory connectivity studies is morphological traits that show predictable geographical variation (Gómez-Díaz and González-Solís 2007). Many species of migratory birds show geographic variation in morphology, including body size (Conklin et al. 2011), wing length (Saracco et al. 2009), bill size (Greenberg et al. 2012), and plumage characteristics (Lehtonen et al. 2009, Paxton et al. 2010). These morphological traits represent a potentially valuable source of data for studying migratory connectivity in many species (Paxton et al. 2010), but to date there have been no attempts to combine morphological traits with other data sources to probabilistically assign individuals to breeding locations.

Here, we combine stable isotope and morphological data to probabilistically assign Wood Thrush (*Hylocichla mustilena*) captured on the wintering grounds to breeding locations. In addition, we use data from breeding Wood Thrush to validate the accuracy and precision of our model and to assess how factors such as age, sex, and breeding origin influence our assignments. Finally, we use these probabilistic assignments to assess the degree of migratory connectivity between breeding and wintering populations. Wood Thrush represent an ideal species to assess these methods because their breeding range spans a large stable isotopic gradient and wing length in this species is positively correlated with latitude (Fig. 1). In addition, Wood Thrush populations in North America have declined by >50% since the 1960s (Evans et al. 2011). Given the extent of this decline, the Wood Thrush is listed as a "Species of Conservation Concern" (U.S. Fish and Wildlife Service 2008), a "priority species" for 30 U.S. states, and is considered threatened by the Committee on Endangered Species of Canada. Accurate estimates of migratory connectivity are critical to identifying the principle threats driving regional population trends and developing effective strategies and partnerships to mitigate these threats (Marra et al. 2011).

METHODS

Data collection

Wood Thrushes were captured during the nonbreeding season (November–March) at six banding stations that were operated as part of the Monitoreo de Sobrevivencia Invernal (MoSI) program between 1999 and 2008 (DeSante et al. 2005). Study areas included Los Tuxtlas in southern Veracruz, Mexico (RBTT); Cerro San Gil (CSGI) in eastern (Izabal) Guatemala; Reserva Privada El Jaguar (JAGU), Reserva Nacional Volcán Mombacho (MOMB), and Esperanza Verde (GUAT) in Nicaragua, and at Centro Agronómico Tropical de Investigación y Enseñanza (CATI) in Costa Rica. Individuals were banded with USGS aluminum bands and aged (second-year, SY; vs. after-second-year, ASY) using plumage criteria and rectrix shape following Pyle (1997). For each individual, we collected morphological data (unflattened wing chord) and sampled feathers (e.g., two outer rectrices, one from each side). These feathers were stored in the Neotropical Migratory Bird Conservation Genetics Project of the University of California, Los Angeles, California, USA (T. B. Smith). Stable isotope analysis of all feather samples was performed at the Smithsonian Stable Isotope Mass Spectrometry Laboratory in Suitland, Maryland, USA (Appendix A).

To assess the degree of migratory connectivity between breeding and nonbreeding populations, we grouped individuals into three broad regions corresponding roughly to the northern, central, and southern portions of the nonbreeding range (Fig. 2). Because sample sizes from several MoSI stations were small (Table 1), these groupings were necessary to detect significant differences from random mixing of breeding populations.

Assignment models

To assign individuals to potential breeding locations, we first created base maps describing the variation in hydrogen isotope abundance in feathers (δ^2H_f) and wing chord (W) across the Wood Thrush breeding range. Given that second-year (SY) Wood Thrush have significantly shorter wings than adults (ASY; $F_{1,\,10079} = 455.50$, $P < 0.001$), we produced separate wing chord base maps for SY and ASY individuals. To estimate the hydrogen isoscape (Appendix C: Fig. C1), we converted a map of expected amount-weighted growing-season precipitation δ^2H values (δ^2H_p; Bowen et al. 2005) to expected feather δ^2H values (δ^2H_f) using the following correction factor: $\delta^2H_f = -175.57 + 0.95\ \delta^2H_p$, which was estimated from a large sample of ground foraging Neotropical migratory songbirds (Hobson et al. 2012). In their analysis, Hobson et al. (2012) found no support for age-based differences in hydrogen isotope discrimination and therefore we did not apply any age-specific correction to the δ^2H values.

To interpolate age-specific spatial variation in Wood Thrush wing morphology, we used unflattened wing chord measurements from 2271 individuals sampled at 64 bird-banding stations operated during the breeding season (May–August) as part of the Monitoring Avian Productivity and Survivorship (MAPS) program between 2002 and 2011 (DeSante and Kaschube 2009; Fig. 1A). We used ordinary kriging with a stable semivariogram model (Nugget = 2.92, Sill = 1.55, Lag = 0.88) to create an interpolated map of range-wide variation in wing chord (Fig. 1A). Specifically, we used mean wing chord values from MAPS sampling locations to predict wing chord across the entire breeding range. We then extracted predicated wing chord values to a 30 × 30 km grid equivalent to that which had been used for stable isotope analyses. Although wing chord varies by sex, we chose not to create sex-specific maps because we did not have information about the sex of nonbreeding birds. While including sex-specific wing chord variation in the model would improve the accuracy and precision of our assignments, assignment rates of known-origin birds were high without this information (see *Validation results*), suggesting that our methods were adequate for estimating the breeding origin of both male and female Wood Thrush. All spatial analyses were done using geostatistical analyst in ArcMap version 10.1 (ESRI 2012).

Assignments of nonbreeding individuals

We first assigned nonbreeding birds to potential breeding locations using isotope values and wing chord separately. To do this, we calculated the likelihood that each raster cell represented the breeding location for each individual using a normal probability density function:

$$f(y* \mid \mu_i, \sigma) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(y* - \mu_i)^2}{2\sigma^2}}$$

where $f(y* \mid \mu_i, \sigma)$ is the likelihood that an individual with δ^2H_f or $W = y*$ originated from cell i; μ_i is the predicted δ^2H_f or W value for cell i; and σ is the standard deviation of δ^2H_f or W values within a single

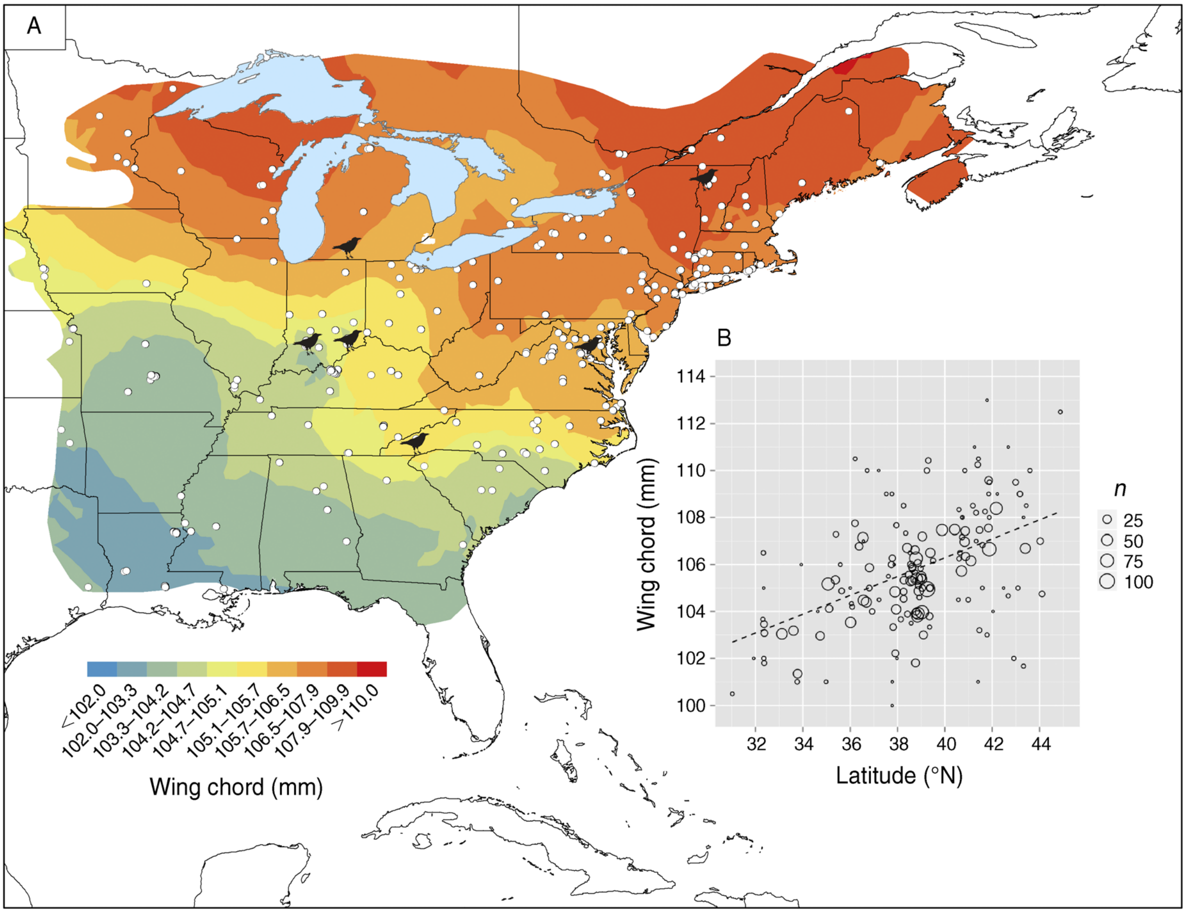

FIG. 1. Sampling locations of feathers (bird icons) and morphological data (white dots) used in validation and to probabilistically assign Wood Thrush (*Hylocichla mustelina*) sampled in nonbreeding areas to their breeding origin. (A) Ordinary kriging shows the spatial pattern of latitudinal variation in Wood Thrush morphology. (B) Wood Thrush wing chord length shows a linear increase with latitude (wing = 90.54 + 0.39 × latitude; $F_{1,4867} = 376.29$, $P < 0.001$, $r^2 = 0.07$). The key indicates that point size is proportional to the number of individuals sampled for morphological data.

breeding site. Wing chord standard deviation was calculated using data collected at the MAPS stations located across the breeding range and was estimated to be 3.3 mm. We estimated the $\delta^2\text{H}_\text{f}$ standard deviation from published values of within-site $\delta^2\text{H}_\text{f}$ variation in Wood Thrush; this SD was assumed to be 10‰ (Powell and Hobson 2006).

Next, we assigned individuals using both stable isotope values and wing chord by estimating the likelihood that each raster cell represented the breeding location of each nonbreeding individual, using a bivariate normal probability function as follows:

$$f(x*, y* \mid \mu_i, \Sigma) = \frac{1}{2\pi\sigma_x\sigma_y\sqrt{1-\rho^2}} \exp\left(-\frac{1}{2(1-\rho^2)}\left[\frac{(x* - \mu_x)^2}{\sigma_x^2} + \frac{(y* - \mu_y)^2}{\sigma_y^2} - \frac{2\rho(x-\mu_x)(y-\mu_y)}{\sigma_x\sigma_y}\right]\right)$$

where $f(x^*, y^* \mid \mu_i, \Sigma)$ is the likelihood that an individual with $\delta^2\text{H}_\text{f} = x^*$ and $W = y^*$ originated from cell i; $\mu_i = \begin{pmatrix}\mu_x \\ \mu_y\end{pmatrix}$ is the mean $\delta^2\text{H}_\text{f}$ and W of cell i; ρ is the correlation between $\delta^2\text{H}_\text{f}$ and W; and

$$\boldsymbol{\Sigma} = \begin{bmatrix} \sigma_x^2 & \rho\sigma_x\sigma_y \\ \rho\sigma_x\sigma_y & \sigma_y^2 \end{bmatrix}$$

is the variance covariance matrix for $\delta^2\text{H}$ and W, which was estimated from the predicted $\delta^2\text{H}$ and W values for each cell across the entire breeding range. All analyses were performed in the R statistical computing environment (R Development Core Team 2008) using the "mnormt" package (Azzalini 2012).

Mapping "likely" breeding origins

For each nonbreeding individual, the likelihoods calculated for the three assignment models (wing chord, isotope, and wing chord + isotope) were rescaled to highest likelihood for that assignment, resulting in

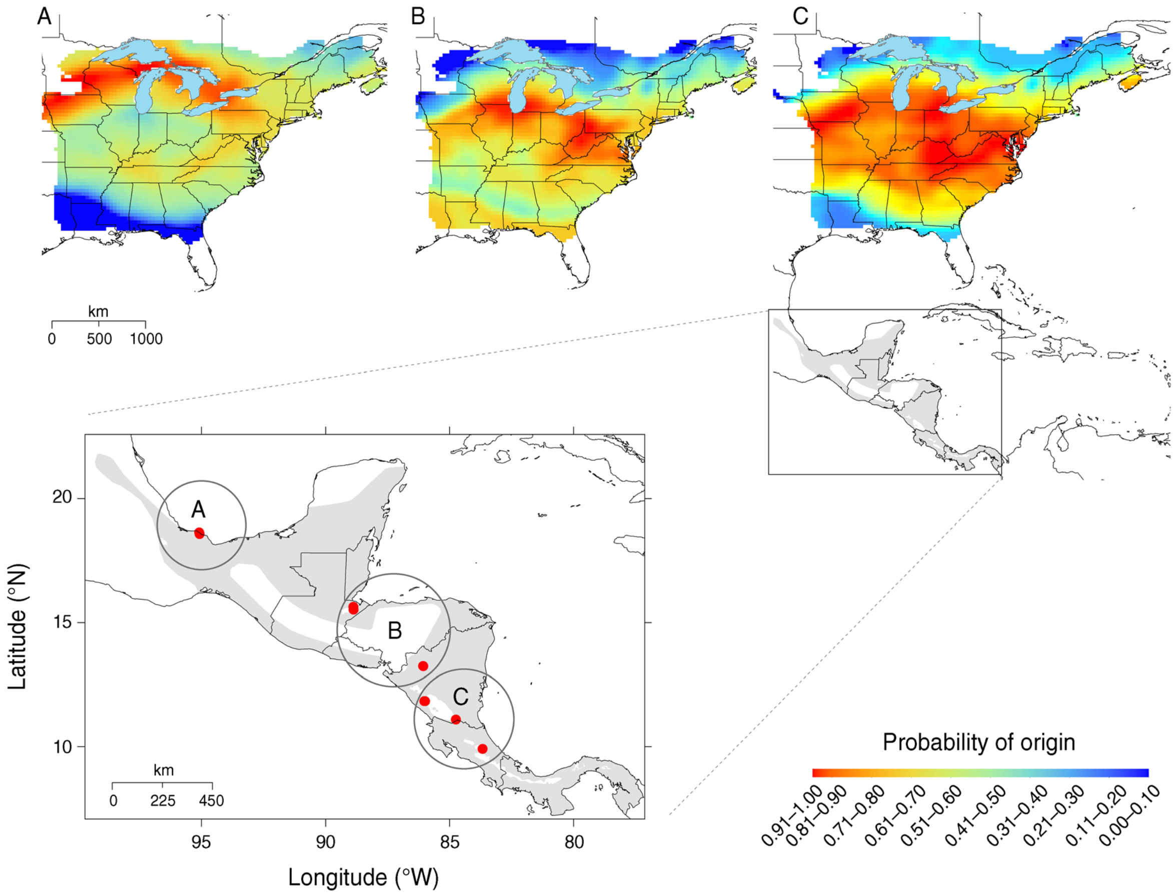

FIG. 2. The predicted probability of Wood Thrush origin using data from stable isotopes and geographic variation in wing morphology for birds sampled in the (A) northern, (B) central, and (C) southern portions of the nonbreeding range (gray shaded area in the inset). Red circles in the nonbreeding range map mark the MoSI (Monitoreo de Sobrevivencia Invernal) stations where feather samples and wing chord measurements were collected for nonbreeding Wood Thrush, i.e., the stations in Table 1.

relative likelihoods that ranged from 0 to 1. We then converted the relative likelihoods to "likely" or "unlikely" breeding locations by assigning cells containing the upper 75% of relative likelihoods a value of "1" and all other cells a value of "0" (Van Wilgenburg and Hobson 2011). This resulted in a binary map for each individual showing the most likely breeding origins based on each assignment model. More stringent thresholds (90%) would result in more cells being identified as likely, resulting in higher accuracy but lower precision, whereas less stringent thresholds (67%) have the opposite effects. We chose to use a 75% threshold to balance this trade-off, but present results using a 67% threshold for comparison.

We then produced overall "connectivity" maps for each nonbreeding region by overlaying the assignment maps of all individuals from that region and summing the number of individuals predicted to have originated within each cell using a raster calculator in ArcMap version 10. To quantify migratory connectivity between breeding and nonbreeding regions, we divided the breeding region into four quadrants (northeast, northwest, southeast, southwest; Appendix C: Fig. C1). For each individual, we calculated the mean likelihood of all raster cells within each quadrant and assigned individuals to the quadrant with the highest mean likelihood. For each nonbreeding region, we then summed these assignments to determine the percentage of individuals assigned to each breeding quadrant. We further used these assignments to test for latitudinal or longitudinal trends in patterns of migration. To test for latitudinal patterns (e.g., chain vs. leap-frog migration), we classified individuals assigned to the northeast and northwest quadrants as "northern" and individuals assigned to the southeast and southwest quadrants as "southern." To test for longitudinal patterns (e.g., migratory divide), we combined the northeast and southeast quadrants and the northwest and northeast quadrants to create "eastern" and "western" regions.

Given the null expectation of complete mixing of breeding populations on the nonbreeding grounds (i.e., no connectivity), the percentage of individuals assigned to each breeding quadrant should be equal to relative breeding abundance of each quadrant (Royle and Rubenstein 2004). Significant differences from this null expectation indicate regions that exhibit stronger connectivity than expected under complete mixing. To estimate the null expectation for our assignments, we used data from the North American Breeding Bird Survey (BBS; Robbins et al. 1986) to estimate the relative abundance of Wood Thrush breeding in each quadrant. Specifically, we used the mean count for each BBS route to compute relative numbers of Wood Thrush counted in each quadrant. Although BBS data suffer from several limitations (Sauer and Link 2011), Wood Thrush are easily detected during the breeding season and BBS surveys cover the entire breeding range. As a result, these data should provide a reasonable estimate of the expected percentages for our breeding quadrants.

Model validation

To assess the accuracy of our assignment models, we conducted a separate analysis using wing chord and isotope data collected from breeding Wood Thrush. Individuals were captured between 2009 and 2011 as part of separate projects at six locations that span the breeding range (bird symbols in Fig. 1A) and represent a mixture of age and sex classes (Table 2). To ensure that individuals were breeding at the location where they were sampled, we only included individuals captured between 1 June and 31 July. We assigned each individual using the models previously described, and individuals were assigned correctly if the raster cell containing the actual breeding location was identified as a likely origin. We estimated the uncertainty of each assignment as the total number of raster cells that were scored as likely breeding locations.

RESULTS

The assignments of nonbreeding individuals to potential breeding locations using stable isotopes and morphology suggest that Wood Thrush exhibit moderate connectivity across their breeding and nonbreeding ranges (Table 3, Fig. 2). Only region A, the westernmost nonbreeding region, had breeding assignments that differed from the null expectation of complete mixing ($\chi^2 = 58.52$, df = 3, $P < 0.001$), indicating that this region had significantly more birds assigned to the northwest quadrant than expected, based on the relative breeding abundance in the northwest. In contrast, the percentage of assignments to each quadrant did not differ from complete mixing in region B ($\chi^2 = 3.67$, df = 3, $P = 0.29$) or in region C ($\chi^2 = 1.16$, df = 3, $P = 0.76$).

When quadrants were paired (i.e., north vs. south and east vs. west), the assignments suggest that Wood Thrush exhibit a weak migratory divide, with western breeding populations more likely to winter in western nonbreeding sites and eastern breeding populations more likely to winter in eastern nonbreeding sites (Table 3). Region A contained more western individuals than expected based on complete mixing ($\chi^2 = 4.34$, df = 1, $P = 0.04$), whereas region B, the most central nonbreeding region, contained nearly equal numbers of eastern and western individuals ($\chi^2 = 0.88$, df = 1, $P = 0.35$). Region C did contain more birds from the eastern half of the breeding range (Table 3), although the proportion of eastern and western individuals did not differ from complete mixing ($\chi^2 = 0.072$, df = 1, $P = 0.79$).

No clear latitudinal migration pattern (e.g., leap-frog vs. chain) emerged from our assignments. Region A did contain more northern individuals than expected based on complete mixing ($\chi^2 = 12.38$, df = 1, $P = 0.004$), but region B ($\chi^2 = 0.13$, df = 1, $P = 0.72$) and region C ($\chi^2 = 1.066$, df = 1, $P = 0.31$) did not. Taken together, our assignments suggest that there is a generally high level of mixing of breeding populations on the nonbreeding grounds, particularly for eastern and southern breeding populations. However, western populations, particularly individuals from the northwestern portion of the breeding range, do appear to show some degree of connectivity during the nonbreeding season.

Validation results

Overall, the assignment rate for the wing chord model (97.5%; Table 4) was significantly higher than the rate of the hydrogen model (80.1%; $\chi^2 = 17.3$, df = 1, $P < 0.01$)

TABLE 1. Summary of nonbreeding sampling regions for Wood Thrush (*Hylocichla mustelina*), with station codes, geographic coordinates, and the number of ASY and SY individuals.

Region	Station	Latitude (°N)	Longitude (°W)	Sample size		
				ASY	SY	Total
A	RBTT	18.58694	95.07722	15	3	18
B	CSGI	15.63889	88.86944	9	3	12
B	JAGU	13.23250	86.05250	5	2	7
C	MOMB	11.83222	86.00833	5	0	5
C	GUAT	11.08639	84.73611	4	3	7
C	CATI	9.89865	83.86944	2	3	5

Notes: Regions and stations are shown in Fig. 2; ASY and SY are after-second-year and second-year birds.

TABLE 2. Summary of validation sampling locations for Wood Thrush, with geographic coordinates and the number of ASY and SY individuals of each sex captured at each Monitoring Avian Productivity and Survival (MAPS) station used to validate our assignment models.

			ASY		SY		
State	Latitude (°N)	Longitude (°W)	Male	Female	Male	Female	Total
North Carolina	35.41114	83.12166	15	3	13	1	32
Virginia	38.70961	77.146699	13	2	11	1	27
Indiana	38.83829	86.82134	24	3	0	1	28
Michigan	42.15833	85.47387	3	3	0	0	6
Vermont	44.50697	73.15053	8	0	19	0	27

and the joint model (74.1%; $\chi^2 = 26.8$, df = 1, $P < 0.01$). The assignment rates did not differ between the hydrogen and joint models ($\chi^2 = 1.53$, df = 1, $P = 0.22$). Assignment rates using the joint model did not differ between age classes ($\chi^2 = 0.42$, df = 1, $P = 0.52$) or between males and females ($\chi^2 = 0.06$, df = 1, $P = 0.94$; Table 5). As expected, the assignment rates were lower when a 67% threshold was used to identify likely breeding locations (Appendix B: Table B1)

The differences in assignment rates were driven mainly by the low assignment rate of North Carolina samples using the hydrogen and joint models (Table 4). The North Carolina site is located within a mountainous area in the western part of the state (Fig. 1), and the high elevations result in predicted hydrogen values that are more depleted than at low-elevation sites at the same latitude (Appendix C: Fig. C1). However, Wood Thrush generally breed only at low elevations (Evans et al. 2011), resulting in hydrogen values that are enriched relative to the predicted values. Thus, many North Carolina individuals were assigned to more southerly locations, even when wing chord was included in the assignments. When the North Carolina samples were excluded, the assignment rates did not differ between the models ($\chi^2 = 1.1$, df = 1, $P = 0.58$).

Although wing chord data alone produced an accurate assignment model, combining the two markers substantially reduced the uncertainty of assignments and increased model precision (mean ± SD number of cells identified as likely: hydrogen only = 2071 ± 586 cells; wing chord only = 2943 ± 586 cells; joint assignment = 1877 ± 592 cells). On average, the joint model resulted in a 37% reduction in the area assigned as "likely" compared to the assignments based on wing chord alone (paired t test: $t = 18.7$, df = 119, $P < 0.01$), and a 10% reduction compared to assignments based on hydrogen alone ($t = 6.73$, df = 119, $P < 0.01$).

DISCUSSION

Quantifying patterns of migratory connectivity is critical to understanding the ecology and evolution of migratory species as well as for creating effective management and conservation strategies. In this study, we present a novel method for quantifying migratory connectivity that combines multiple intrinsic data sources to probabilistically assign individuals to breeding locations. Our results for Wood Thrush demonstrate that, despite relatively high levels of mixing across their breeding and nonbreeding ranges, there is evidence of moderate connectivity along an east–west gradient. This pattern is consistent with previously reported east–west divides in several other species of Nearctic–Neotropical migrants (Smith et al. 2005, Boulet et al. 2006, Norris et al. 2006). Our ability to detect longitudinal migration patterns is surprising, given that both hydrogen isotopes and wing chord are considered latitudinal markers (Hobson and Wassenaar 1997). However, while both markers vary primarily along a north–south gradient, the clines of each marker run at a slight angle (Fig. 1; Appendix C: Fig. C1), and our results suggest that this amount of longitudinal information is sufficient to detect eastern vs. western migration patterns.

The longitudinal patterns of migratory connectivity described here for Wood Thrush are largely consistent with data from other sources (e.g., geolocators; Stutchbury et al. 2009, Stanley et al. 2012). Previous studies, however, were largely based on single breeding populations and as such have limited ability to assess range-wide linkages between breeding and wintering sites (McKinnon et al. 2013). The use of historical migration routes is one hypothesis that might explain east–west

TABLE 3. Summary of nonbreeding assignments for Wood Thrush: the percentage of individuals from each nonbreeding region assigned to each breeding quadrant.

Nonbreeding region	Northeast	Northwest	Southeast	Southwest
A	15.0 (3/20)	55.0 (11/20)	20.0 (4/20)	10.0 (2/20)
B	31.6 (6/19)	5.3 (1/19)	15.8 (3/19)	47.3 (9/19)
C	33.3 (6/18)	11.1 (2/18)	27.8 (5/18)	27.8 (5/18)

Note: In parentheses are the number of individuals assigned and the total sample size.

TABLE 4. Results of validation assignments for Wood Thrush: the percentage of individuals correctly assigned to their breeding location.

State	Hydrogen only	Wing chord only	Joint
North Carolina	40.1 (13/32)	100 (32/32)	25.0 (8/32)
Virginia	85.2 (23/27)	92.6 (25/27)	81.5 (22/27)
Indiana	96.4 (27/28)	89.2 (25/28)	96.4 (27/28)
Michigan	100 (6/6)	100 (6/6)	100 (6/6)
Vermont	100 (27/27)	96.3 (26/27)	96.3 (26/27)
Total	80.1 (97/120)	97.5 (117/120)	74.1 (89/120)

Note: In parentheses are the number of individuals correctly assigned and the total sample size.

patterns of connectivity in Wood Thrush. Populations may be genetically predisposed to use migratory routes established prior to population range expansion (Delmore et al. 2012), and these "traditional" routes may be reinforced and/or constrained by contemporary weather conditions and the associated costs of using alternatives (Able 1973, Lundberg and Alerstam 1986). Data from both Swainson's Thrush and Wood Thrush appear to support the idea that breeding longitude is a good predictor of fall migration routes and, to a lesser extent, subsequent wintering areas (Stanley et al. 2012, Cormier et al. 2013; C. Q. Stanley et al., *unpublished data*). Regardless of the exact mechanisms that maintain patterns of longitudinal migratory connectivity, these linkages probably reflect both ecological and evolutionary factors.

Accuracy and precision in probabilistic assignment models

Validation is critical to testing the accuracy and precision of assignment models; our validation tests confirm that our models correctly assigned most individuals to their breeding location regardless of age or sex. Interestingly, although the assignment rate of our joint model was similar to that for other taxa (e.g., birds, Chabot et al. [2012]; sea turtles, Stewart et al. [2013]), the assignments based on wing chord alone were often more accurate but less precise than the joint assignments. Incorrect assignments based on the joint model tended to occur when individuals had strong disagreement between the markers. For example, five individuals from the North Carolina population had unusually enriched isotope values (indicating southern origin), but unusually long wing chord (indicating northern origin). In each case, the assignments based on only one marker correctly identified the actual breeding location, yet in each case the true site was at the periphery of the area identified as the "likely" origin. When the markers were combined, the relative likelihood for the true location dropped below the critical threshold required for correct assignment, leading to incorrect assignment for these individuals using the joint model.

To improve the spatial resolution of connectivity maps, assignment models should aim to simultaneously maximize accuracy and precision because highly accurate but imprecise assignments provide limited information about the degree of migratory connectivity and the development of regional conservation priorities (Martin et al. 2007). While combined data sources in the joint model led to a slight reduction in the accuracy of assignments for some locations (e.g., North Carolina), the use of multiple markers led to a large increase in the precision of assignments. For example, our assignments based on wing chord alone had very high accuracy (97.5%), but very low precision (mean ± SD = 2943 ± 586). While precision was better when using isotopes alone (2071 ± 586 cells identified as "likely" origin), combining the markers resulted in a 37% increase in precision of wing chord alone and a 10% increase over isotopes alone. Similar increases in precision have been found in other studies that make probabilistic assignments using multiple data sources. For example, combining stable isotope data with band recoveries resulted in a 67% increase in the precision of assignments of White-throated Sparrows (*Zonotrichia albicollis*) compared to assignments based on isotopes alone (Van Wilgenburg and Hobson 2011). Similarly, Chabot et al. (2012) found that assignments of Loggerhead Shrikes (*Lanius ludovicianus*) based on both genetic data and stable isotopes led to a three- to fivefold increase in precision compared to either marker alone. Ultimately, given the balance between maximizing region-specific accuracy and range-wide

TABLE 5. Age- and sex-specific assignment rates for Wood Thrush using joint assignment: the percentage of individuals correctly assigned to their breeding location.

State	ASY correct	SY correct	Male correct	Female correct
North Carolina	16.6 (3/18)	35.7 (5/14)	28.6 (8/28)	0 (0/4)
Virginia	73.3 (11/15)	91.7 (11/12)	79.2 (19/24)	100 (3/3)
Indiana	92.5 (25/27)	100 (1/1)	91.2 (22/24)	100 (4/4)
Michigan	100 (6/6)	NA (0/0)	100 (3/3)	100 (3/3)
Vermont	100 (8/8)	94.7 (18/19)	96.3 (26/27)	NA (0/0)
Total	68.7 (46/67)	76.1 (35/46)	73.6 (78/106)	76.9 (10/13)

Note: In parentheses are the number of individuals correctly assigned and the total sample size.

precision, we argue that the increased precision associated with the joint model justifies the slight decrease in accuracy compared to the use of either marker alone.

Despite the strong performance of our model, there are a number of important caveats to consider when making probabilistic assignments with isotope and morphology data. First, the accuracy of our validation samples could have been influenced by the dispersal of individuals between breeding locations (Chabot et al. 2012). Results of our validation assignments, however, only would have been impacted by long-distance dispersal events (roughly >100 km), given the spatial resolution of our markers. Given that long-distance dispersal of this magnitude is generally rare (Tittler et al. 2009), we expect that dispersal events probably had a small impact on the accuracy of our validation assignments. Furthermore, while long-distance dispersal may have lowered the accuracy of our validation samples, dispersal between breeding sites would not influence the assignment of birds sampled during the nonbreeding season, and therefore dispersal does not impact our conclusions about migratory connectivity.

A second factor that could influence both the accuracy and precision of our assignments is site-specific individual variation in isotope signatures and wing morphometrics. Several studies have shown that δ^2H_f feather values from passerines known to have originated at the same location can vary by as much as 10–15‰ (Powell and Hobson 2006, Langin et al. 2007; C. Rushing, *unpublished data*) and wing chord can show similar within-site variation. Some of this variation may be due to age or sex differences in isotope discrimination or body size. For example, there is some evidence that hydrogen isotope discrimination varies between age classes, leading several studies to apply age-specific correction factors (Haché et al. 2012, Studds et al. 2012). However, based on the results of Hobson et al. (2012), we chose not to apply any age corrections to our base map. The fact that assignment rates were similar for both ASY and SY individuals confirms that our models were robust to any age-specific isotope discriminations. Although our models were able to correct for age, we were unable to account for sex-specific variation because thrushes on the wintering grounds cannot be accurately sexed using plumage characters alone. Including sex-specific wing chord predictions in our model would almost certainly improve the accuracy and precision of our assignments. Regardless, even after controlling for age and sex, residual within-site variation (Langin et al. 2007) will still remain a key source of error for both accuracy and precision. As probabilistic assignment approaches advance, the incorporation of multiple isotope markers, particularly those that vary longitudinally (Sellick et al. 2009), and the use of informative priors in Bayesian models (Royle and Rubenstein 2004, Van Wilgenburg and Hobson 2011, Hallworth et al. 2013), will undoubtedly help to improve model performance.

Using morphological variation to inform migratory connectivity

Evolutionary biologists and taxonomists alike have long been interested in characterizing and explaining geographic variation in avian morphology across species' ranges including along latitudinal or altitudinal gradients (Mayr 1956, Hamilton 1961, Browning 1994, Arizaga et al. 2006, Nudds and Oswald 2007, McKay 2008, Rising et al. 2009, Paxton et al. 2010, Greenberg et al. 2012). Moreover, a substantial body of work has characterized how natural selection (Greenberg et al. 1998, Lehtonen et al. 2009) and sexual selection (Møller 1995, Dunn et al. 2008, Potti and Canal 2011) have shaped phenotypic variation. Although the ecological and evolutionary forces behind these patterns remain controversial (Watt et al. 2010), these investigations have produced a wealth of data that can provide valuable information for geographic assignments (Conklin et al. 2011). Here, we have demonstrated that geographic variation in morphology has the potential to greatly improve estimates of migratory connectivity when combined with other markers, particularly in cases where gradients of morphological variation complement gradients of other markers (e.g., isotopes or genetic data).

Morphological data offer several distinct advantages for quantifying migratory connectivity. First, geographic variation of many traits has already been described for many species, providing researchers with readily accessible information for conducting assignments (McKay 2008). Second, in cases where geographic variation has not been adequately quantified, base maps can be created using data from museum collections (Pyke and Ehrlich 2010). Third, morphological data are often easier and less expensive to collect than other forms of data, making it feasible to sample a large number of individuals. Furthermore, many relevant traits (e.g., body size, wing length) are measured as part of standard sampling protocols, making it possible to conduct assignments using existing data sets. Given the widespread morphological variation observed in many species, the wealth of existing data, and the advantages just outlined, morphological traits represent a tremendously valuable, but largely untapped, resource for quantifying patterns of migratory connectivity.

Although the enigmatic declines of migratory songbirds have been well publicized, closer examination reveals that most species show substantial variation in regional population trends, with some areas showing sharp declines while others have remained stable or even increased (Faaborg et al. 2010). Without accurate information about migratory connectivity, it is impossible to determine where and when populations face limiting factors or to develop effective management strategies to mitigate regional threats (Martin et al.

2007, Marra et al. 2011). Here, we demonstrate that combining intrinsic data sources is a useful approach for increasing the spatial precision of range-wide migratory connectivity estimates. Further development of these methods, for example by combining intrinsic markers with novel extrinsic markers (e.g., geolocators), promises to advance our understanding of the basic ecology and evolution of long-distance migrant birds, and will allow strategic habitat conservation to protect declining populations.

Acknowledgments

Thanks to T. B. Smith for providing feather samples archived as part of the Neotropical Migrant Conservation Genetics Project (NMCGP) of the University of California at Los Angeles. We thank the many MAPS station operators who have contributed wing chord data. Individual MoSI contributors who provided feather samples and wing chord data include O. Arroliga (GUAT; Amigos del Rio San Juan), R. Coates and D. Curiel (RBTT; Universidad Nacional Autónoma de México), A. Cerezo (CSGI; FUNDAECO), J. M. Zolotoff (MOMB; Fundación Cocibolca), L. and G. Duriaux Chavarria (JAGU; Reserva Privada El Jaguar), and F. De Clerck and A. Martínez (CATI; Centro Agronómico Tropical de Investigación y Enseñanza). This is contribution no. 464 of The Institute for Bird Populations. Funding provided by the Strategic Environmental Resource and Development Program (SERDP Award RC-2121).

Literature Cited

Able, K. P. 1973. The role of weather variables and flight direction in determining the magnitude of nocturnal bird migration. Ecology 54:1031–1041.

Arizaga, J., F. Campos, and D. Alonso. 2006. Variations in wing morphology among subspecies might reflect different migration distances in Bluethroat. Ornis Fennica 83:162–169.

Azzalini, G. 2012. Package 'mnormt': The multivariate normal and *t* distributions. R package version 1.4-5. http://cran.r-project.org/web/packages/mnormt/index.html

Boulet, M., H. L. Gibbs, and K. A. Hobson. 2006. Integrated analysis of genetic, stable isotope, and banding data reveal migratory connectivity and flyways in the northern Yellow Warbler (*Dendroica petechia*; *aestiva* group). Ornithological Monographs 61:29–78.

Bowen, G. J., L. I. Wassenaar, and K. A. Hobson. 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. Oecologia 143:337–348.

Browning, M. R. 1994. A taxonomic review of *Dendroica petechia* (yellow warbler) (Aves: Parulinae). Proceedings of the Biological Society of Washington 107:27–51.

Chabot, A. A., K. A. Hobson, S. L. Van Wilgenburg, G. J. McQuat, and S. C. Lougheed. 2012. Advances in linking wintering migrant birds to their breeding-ground origins using combined analyses of genetic and stable isotope markers. PloS One 7(8):e43627.

Clegg, S. M., J. F. Kelly, M. Kimura, and T. B. Smith. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's Warbler (*Wilsonia pusilla*). Molecular Ecology 12:819–830.

Colbeck, G. J., H. L. Gibbs, P. P. Marra, K. A. Hobson, and M. S. Webster. 2008. Phylogeography of a widespread North American migratory songbird (*Setophaga ruticilla*). Journal of Heredity 99:453–463.

Combreau, O., S. Riou, J. Judas, M. Lawrence, and F. Launay. 2011. Migratory pathways and connectivity in Asian houbara bustards: evidence from 15 years of satellite tracking. PloS One 6(6):e20570.

Conklin, J. R., P. F. Battley, M. A. Potter, and D. R. Ruthrauff. 2011. Geographic variation in morphology of Alaska-breeding Bar-tailed Godwits (*Limosa lapponica*) is not maintained on their nonbreeding grounds in New Zealand. Auk 128:363–373.

Cormier, R. L., D. L. Humple, T. Gardali, and N. E. Seavy. 2013. Light-level geologgers reveal strong migratory connectivity and within-winter movements for a coastal California Swainson's Thrush (*Catharus ustulatus*) population. Auk 130:283–290.

Delmore, K. E., J. W. Fox, and D. E. Irwin. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society B 279:4582–4589.

DeSante, D. F., and D. R. Kaschube. 2009. The Monitoring Avian Productivity and Survivorship (MAPS) program 2004, 2005, and 2006 report. Bird Populations 9:86–169.

DeSante, D. F., T. S. Sillett, R. B. Siegel, J. F. Saracco, C. A. Romo de Vivar Alvarez, S. Morales, A. Cerezo, D. R. Kaschube, M. Grosselet, and Míla. B. 2005. MoSI (Monitoreo de Sobrevivencia Invernal): assessing habitat-specific overwintering survival of Nearctic–Neotropical migratory landbirds. Pages 926–936 *in* C. J. Ralph and T. D. Rich, editors. Bird conservation implementation and integration in the Americas. U.S. Forest Service General Technical Report PSW-GTR-191.

Dunn, E. H., K. A. Hobson, L. I. Wassenaar, D. J. Hussell, and M. L. Allen. 2006. Identification of summer origins of songbirds migrating through southern Canada in autumn. Avian Conservation and Ecology 1:4–25.

Dunn, P. O., L. A. Whittingham, C. R. Freeman-Gallant, and J. DeCoste. 2008. Geographic variation in the function of ornaments in the common yellowthroat, *Geothlypis trichas*. Journal of Avian Biology 39:66–72.

ESRI. 2012. ArcMap v. 10.1. Environmental Systems Research Institute, Redlands, California, USA.

Evans, M., E. Gow, R. R. Roth, M. S. Johnson, and T. J. Underwood. 2011. Wood Thrush (*Hylocichla mustelina*). Number 246 in A. Poole, editor. Birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. doi:10.2173/bna.246

Faaborg, J., et al. 2010. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Gómez-Díaz, E., and J. González-Solís. 2007. Geographic assignment of seabirds to their origin: combining morphologic, genetic, and biogeochemical analyses. Ecological Applications 17:1484–1498.

Greenberg, R., V. Cadena, R. M. Danner, and G. Tattersall. 2012. Heat loss may explain bill size differences between birds occupying different habitats. PloS One 7(7):e40933.

Greenberg, R., P. J. Cordero, S. Droege, and R. C. Fleischer. 1998. Morphological adaptation with no mitochondrial DNA differentiation in the coastal plain Swamp Sparrow. Auk 115:706–712.

Haché, S., K. A. Hobson, M. A. Villard, and E. M. Bayne. 2012. Assigning birds to geographic origin using feather hydrogen isotope ratios (δ^2H): importance of year, age, and habitat. Canadian Journal of Zoology 90:722–728.

Hallworth, M. T., C. E. Studds, T. S. Sillett, and P. P. Marra. 2013. Do archival light-level geolocators and stable hydrogen isotopes provide comparable estimates of breeding-ground origin? Auk 130:273–282.

Hamilton, T. H. 1961. The adaptive significances of intraspecific trends of variation in wing length and body size among bird species. Evolution 15:180–195.

Hobson, K. A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. Diversity and Distributions 11:157–164.

Hobson, K. A. 2011. Isotopic ornithology: a perspective. Journal of Ornithology 152:49–66.

Hobson, K. A., S. H. DeMent, S. L. Van Wilgenburg, and L. I. Wassenaar. 2009. Origins of American Kestrels wintering at two southern U.S. sites: an investigation using stable-isotope (δD, δ^{18}O) methods. Journal of Raptor Research 43:325–337.

Hobson, K. A., S. L. Van Wilenburg, L. I. Wassenaar, and K. Larson. 2012. Linking hydrogen isotopes in feathers and precipitation: sources of variance and consequences for assignment to isoscapes. PLoS ONE 7(4):e35137.

Hobson, K. A., and L. I. Wassenaar. 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. Oecologia 109:142–148.

Hobson, K. A., and L. I. Wassenaar. 2008. Tracking animal migration with stable isotopes. Volume 2. Academic Press, New York, New York, USA.

Hobson, K. A., L. I. Wassenaar, and E. Bayne. 2004. Using isotopic variance to detect long-distance dispersal and philopatry in birds: an example with Ovenbirds and American Redstarts. Condor 106:732–743.

Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447–461.

Irwin, D. E., J. H. Irwin, and T. B. Smith. 2011. Genetic variation and seasonal migratory connectivity in Wilson's warblers (*Wilsonia pusilla*): species-level differences in nuclear DNA between western and eastern populations. Molecular Ecology 20:3102–3115.

Kelly, J. F., K. C. Ruegg, and T. B. Smith. 2005. Combining isotopic and genetic markers to identify breeding origins of migrant birds. Ecological Applications 15:1487–1494.

Langin, K. M., M. W. Reudink, P. P. Marra, D. R. Norris, T. K. Kyser, and L. M. Ratcliffe. 2007. Hydrogen isotopic variation in migratory bird tissues of known origin: implications for geographic assignment. Oecologia 152:449–457.

Lehtonen, P. K., et al. 2009. Geographic patterns of genetic differentiation and plumage colour variation are different in the pied flycatcher (*Ficedula hypoleuca*). Molecular Ecology 18:4463–4476.

Lundberg, S., and T. Alerstam. 1986. Bird migration patterns: Conditions for stable geographical population segregation. Journal of Theoretical Biology 123:403–414.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird using stable carbon isotopes. Science 282:1884–1886.

Marra, P. P., D. Hunter, and A. M. Perrault. 2011. Migratory connectivity and the conservation of migratory animals. Environmental Law 41:317–363.

Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris. 2007. Optimal conservation of migratory species. PLoS ONE 2:751–755.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution 10:105–108.

McKay, B. D. 2008. Phenotypic variation is clinal in the Yellow-throated Warbler. Condor 110:569–574.

McKinnon, E. A., K. C. Fraser, and B. J. M. Stutchbury. 2013. New discoveries in landbird migration using geolocators and a flight plan for the future. Auk 130:1–12.

Møller, A. P. 1995. Sexual selection in the barn swallow (*Hirundo rustica*). V. Geographic variation in ornament size. Journal of Evolutionary Biology 8:3–19.

Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. Migratory connectivity of a widely distributed Nearctic–Neotropical songbird, the American Redstart (*Setophaga ruticilla*). Ornithological Monographs 61:14–28.

Nudds, R. L., and S. A. Oswald. 2007. An interspecific test of Allen's rule: Evolutionary implications for endothermic species. Evolution 61:2839–2848.

Pain, D. J., R. E. Green, B. Gieβing, A. Kozulin, A. Poluda, U. Ottosson, M. Flade, and G. M. Hilton. 2004. Using stable isotopes to investigate migratory connectivity of the globally threatened aquatic warbler *Acrocephalus paludicola*. Oecologia 138:168–174.

Paxton, E. H., M. K. Sogge, T. J. Koronkiewicz, M. A. McLeod, and T. C. Theimer. 2010. Geographic variation in the plumage coloration of willow flycatchers *Empidonax traillii*. Journal of Avian Biology 41:128–138.

Potti, J., and D. Canal. 2011. Heritability and genetic correlation between the sexes in a songbird sexual ornament. Heredity 106:945–954.

Powell, L. A., and K. A. Hobson. 2006. Enriched feather hydrogen isotope values for Wood Thrushes sampled in Georgia, USA, during the breeding season: implications for quantifying dispersal. Canadian Journal of Zoology 84:1331–1338.

Pyke, G. H., and P. R. Ehrlich. 2010. Biological collections and ecological/environmental research: a review, some observations and a look to the future. Biological Reviews 85:247–266.

Pyle, P. 1997. Identification guide to North American birds, Part 1. Slate Creek Press, Bolinas, California, USA.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rising, J. D., D. A. Jackson, and H. B. Fokidis. 2009. Geographic variation in plumage pattern and coloration of Savannah Sparrows. Wilson Journal of Ornithology 121:253–264.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965–1979. USDI Fish and Wildlife Service, Washington, D.C., USA.

Royle, J. A., and D. R. Rubenstein. 2004. The role of species abundance in determining breeding origins of migratory birds with stable isotopes. Ecological Applications 14:1780–1788.

Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology and Evolution 19:256–263.

Rundel, C. W., et al. 2013. Novel statistical methods for integrating genetic and stable isotope data to infer individual-level migratory connectivity. Molecular Ecology 22:4163–4176.

Runge, M., and P. P. Marra. 2005. A demographic model for a migratory passerine bird: population dynamics of the American redstart. Pages 375–389 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of temperate–tropical migration systems. Johns Hopkins University Press, Baltimore, Maryland, USA.

Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark–recapture data. Auk 128:448–453.

Saracco, J. F., D. F. DeSante, M. P. Nott, and D. R. Kaschube. 2009. Using the MAPS and MoSI programs to monitor landbirds and inform conservation. Pages 651–658 *in* T. D. Rich, C. D. Thompson, D. Demarest, and C. Arizmendi, editors. Proceedings of the Fourth International Partners in Flight Conference. Partners in Flight. University of Texas-Pan American Press, Edinburg, Texas, USA. http://www.partnersinflight.org/pubs/mcallenproc/articles/pif09_monitoring/saracco_1_pif09.pdf

Sarasola, J. H., J. J. Negro, K. A. Hobson, G. R. Bortolotti, and K. L. Bildstein. 2008. Can a 'wintering area effect' explain population status of Swainson's hawks? A stable isotope approach. Diversity and Distributions 14:686–691.

Sauer, J. R., and W. A. Link. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. Auk 128:87–98.

Sellick, M. J., T. K. Kyser, M. B. Wunder, D. Chipley, and D. R. Norris. 2009. Geographic variation of strontium and hydrogen isotopes in avian tissue: implications for tracking migration and dispersal. PloS ONE 4(3):e4735.

Smith, T. B., S. M. Clegg, M. Kimura, K. C. Ruegg, B. Mila, and I. J. Lovette. 2005. Molecular genetic approaches to linking breeding and overwintering areas in five Neotropical migrant passerines. Pages 222–234 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA.

Stanley, C. Q., M. MacPherson, K. C. Fraser, E. A. McKinnon, and B. J. M. Stutchbury. 2012. Repeat tracking of individual songbirds reveals consistent timing but flexibility in route. PLoS ONE 7(7):e40688.

Stewart, K. R., M. C. James, S. Roden, and P. H. Dutton. 2013. Assignment tests, telemetry and tag–recapture data converge to identify natal origins of leatherback turtles foraging in Atlantic Canadian waters. Journal of Animal Ecology 82:791–803.

Studds, C. E., K. P. McFarland, Y. Aubry, C. C. Rimmer, K. A. Hobson, P. P. Marra, and L. I. Wassenaar. 2012. Stable-hydrogen isotope measures of natal dispersal reflect observed population declines in a threatened migratory songbird. Diversity and Distributions 18:919–930.

Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration using geolocators. Science 323:896.

Szép, T., K. A. Hobson, J. Vallner, S. E. Piper, B. Kovács, D. Z. Szabó, and A. P. Møller. 2009. Comparison of trace element and stable isotope approaches to the study of migratory connectivity: an example using two hirundine species breeding in Europe and wintering in Africa. Journal of Ornithology 150:621–636.

Tittler, R., M. A. Villard, and L. Fahrig. 2009. How far do songbirds disperse? Ecography 32:1051–1061.

U.S. Fish and Wildlife Service. 2008. Birds of Conservation Concern 2008. United States Department of Interior, U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia, USA. http://www.fws.gov/migratorybirds/NewReportsPublications/SpecialTopics/BCC2008/BCC2008.pdf

Van Wilgenburg, S. L., and K. A. Hobson. 2011. Combining stable-isotope (δD) and band recovery data to improve probabilistic assignment of migratory birds to origin. Ecological Applications 21:1340–1351.

Watt, C., S. Mitchell, and V. Salewski. 2010. Bergmann's rule; a concept cluster? Oikos 119:89–100.

Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of temperate–tropical migration systems. Johns Hopkins University Press, Baltimore, Maryland, USA.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

Wunder, M. B., C. L. Kester, F. L. Knopf, and R. O. Rye. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. Oecologia 144:607–617.

SUPPLEMENTAL MATERIAL

Appendix A

Description of stable isotope analysis methods (*Ecological Archives* A024-027-A1).

Appendix B

Comparison of assignment rates under 67% and 75% thresholds for identifying "likely" vs. "unlikely" breeding locations (*Ecological Archives* A024-027-A2).

Appendix C

The δ^2H isoscape, feather sampling locations (bird icons) and the quadrants used in validation and to quantifying range wide migratory connectivity for Wood Thrush (*Ecological Archives* A024-027-A3).

Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2015, **84,** 1469–1479 doi: 10.1111/1365-2656.12395

Habitat features and long-distance dispersal modify the use of social information by a long-distance migratory bird

Clark S. Rushing[1,2]*, Michele R. Dudash[1] and Peter P. Marra[2]

[1]Graduate Program in Behavior, Ecology, Evolution, and Systematics 2101 Bioscience Research Building, University of Maryland, College Park, MD 20742, USA; and [2]Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, PO Box 37012 MRC 5503, Washington, DC 20013-7012, USA

Summary

1. The processes by which individuals select breeding sites have important consequences for individual fitness as well as population- and community-dynamics. Although there is increasing evidence that many animal species use information acquired from conspecifics to assess the suitability of potential breeding sites, little is known about how the use of this social information is modified by biotic and abiotic conditions.

2. We used an automated playback experiment to simulate two types of social information, post-breeding public information and pre-breeding location cues, to determine the relative importance of these cues for breeding site selection by a migratory songbird, the American redstart (*Setophaga ruticilla*). In addition, we used stable hydrogen isotopes to determine the dispersal status of individuals that responded to our experimental treatments and quantify whether long-distance dispersers use different social cues to select breeding sites compared to philopatric individuals.

3. We found that points that received pre-breeding location cue treatments were significantly more likely to be settled by redstarts than control points that received no playback. However, we found no evidence the redstarts used post-breeding public information gathered during one season to select breeding sites the following year. Breeding site habitat structure was also a strong predictor of settlement probability, indicating that redstarts modified the use of social information based on habitat cues. Furthermore, stable hydrogen isotope signatures from individuals that responded to location cue treatments suggest that long-distance dispersers may rely more heavily on these cues than local recruits.

4. Collectively, these results indicate that redstarts use multiple sources of information to select breeding sites, which could buffer individuals from selecting suboptimal sites when they breed in unfamiliar locations or when habitat quality becomes decoupled from social cues.

Key-words: conspecific attraction, deuterium, habitat selection, location cues, public information, *Setophaga ruticilla*, social information

Introduction

The ability to locate and select high-quality breeding sites is a key behavioural process that links individual fitness to population- and community-level dynamics, including population regulation (Fretwell & Lucas 1970; Pulliam 1988), community assembly (Fletcher 2008; Betts, Nocera & Hadley 2010) and maintaining biological diversity (Ward & Schlossberg 2004). Understanding the cues that individuals use to assess and select breeding sites is thus a central question in ecology, evolution and conservation (Morris 2003; Danchin *et al.* 2004; Ahlering & Faaborg 2006). In recent decades, empirical research has demonstrated that information acquired from conspecifics, termed *social information*, is widely used by many species to assess the quality of potential breeding sites (Reed *et al.* 1999; Valone 2007). Compared to other sources of information (e.g. habitat features or previous reproductive success), social information is relatively efficient to collect, can provide information about habitat quality even when

*Correspondence author. E-mail: rushingc@si.edu the features that influence fitness are not apparent, and is available to most individuals regardless of age or reproductive experience (Szymkowiak 2013). However, not all types of social information are equally reliable and understanding when and under what conditions individuals use different types of social information remains poorly understood (Doligez *et al.* 2003; Danchin *et al.* 2004; Stamps & Krishnan 2005).

Social information is generally divided into two categories: information about the presence/absence of conspecifics, termed *location cues*, and information about the reproductive performance of conspecifics, termed *public information* (Danchin *et al.* 2004). When the quality of breeding sites is predictable across years, both cues can provide information about the location of suitable breeding sites. However, while the presence of breeding individuals is generally associated with suitable habitat, location cues do not provide direct information about the relative quality of different sites, and under certain circumstances, it is possible for location cues to become uncoupled from habitat quality (i.e. ecological traps, Schlaepfer, Runge & Sherman 2002). In contrast, because public information is based directly on conspecific performance, it is generally a highly reliable cue for assessing breeding site quality. For this reason, public information should be favoured over location cues in stable environments (Doligez *et al.* 2003). Despite this prediction, empirical studies have demonstrated that location cues are widely used by many species (e.g. Serrano *et al.* 2004; Ahlering, Johnson & Faaborg 2006; Szostek, Schaub & Becker 2014). Explaining the coexistence of these two strategies is an important step to developing a general theory of breeding site selection (Szymkowiak 2013).

Several hypotheses may explain why individuals use location cues even when public information provides more reliable information about breeding site quality. First, when all individuals in a population breed synchronously, young individuals do not have the opportunity to gather public information (Nocera, Forbes & Giraldeau 2006) and may be forced to rely on location cues (Doligez *et al.* 2004). Secondly, dispersers forfeit any previously acquired public information when they move to new locations, and therefore, immigrants may be more reliant on location cues than philopatric individuals (Szostek, Schaub & Becker 2014). Although interspecific comparisons of social information use provide some empirical support for both hypotheses (Reed *et al.* 1999; Stamps & Krishnan 2005), the dynamics of populations are ultimately influenced by intraspecific variation in habitat selection behaviour (Kristan 2003). Therefore, linking individual behaviour to population dynamics requires understanding the causes of intraspecific variation in breeding site selection. Few studies, however, have simultaneously quantified the relative importance of public information and location cues for individuals within the same population (but see Doligez *et al.* 2004; Nocera, Forbes & Giraldeau 2006).

In this study, we simulated post-breeding public information and pre-breeding location cues to experimentally test the relative importance of each cue for breeding site selection in a migratory songbird, the American redstart (*Setophaga ruticilla*). This experimental simulation allowed us to test the following predictions:

1. Redstarts use both pre-breeding location cues and post-breeding public information to select breeding sites: Several studies have documented the use of pre-breeding location cues by American redstarts (Hahn & Silverman 2006; Fletcher 2007), and therefore, we predicted that this would be an important source of social information for birds in our population. The use of post-breeding public information by redstarts has not been studied, but Betts *et al.* (2008) experimentally demonstrated that individuals of the closely related black-throated blue warbler (*Setophaga caerulescens*) monitor the reproductive performance of conspecifics and use this information to select breeding sites the following year. Given the close phylogenetic relationship between these two species (Lovette *et al.* 2010) and the similarity of their breeding habitat, we predicted that redstarts would also use post-breeding public information to select breeding sites.
2. Pre-breeding location cues are a more important source of information than post-breeding public information: Black-throated blue warblers often produce two broods per season, and this asynchrony provides individuals from early broods the opportunity to gather public information from the territories of successful second broods (Betts *et al.* 2008). In contrast, because redstarts are obligate single brooders (Sherry & Holmes 1997), their short, synchronous breeding season may prevent newly fledged redstarts from gathering public information (Nocera, Forbes & Giraldeau 2006). Therefore, we predicted that post-breeding public information would be a less important source of social information than pre-breeding location cues for redstarts.
3. The use of social information differs between adults and yearlings due to asynchronous opportunities to collect public information: Although newly fledged redstarts may not have the opportunity to collect public information, many yearling males in our population remain unmated throughout the breeding season (C. Rushing pers. obs.) and these individuals provide a potential pool of prospectors that could gather and use post-breeding public information when they return as adults the following year (Doligez *et al.* 2004). Therefore, we predicted that adults would be more likely than yearlings to settle in response to post-breeding public information treatments, whereas pre-breeding location cues would be more important for yearlings attempting to breed for the first time.
4. Long-distance dispersal modifies the use of social information cues: Because dispersing individuals

cannot rely on post-breeding public information gathered the previous year, we predicted that immigrants would be more likely to use pre-breeding location cues than philopatric individuals.

Materials and methods

STUDY SPECIES AND EXPERIMENTAL DESIGN

American redstarts are long-distance neotropical migratory songbirds that breed throughout North America and winter in the Caribbean and Latin America (Sherry & Holmes 1997). Since 2009, we have studied a large population of redstarts breeding at the Patuxent Research Refuge in Laurel, Maryland, USA (39° 04'N, 76° 47'W). The 250-ha study area consists primarily of beech-dominated bottomland forests adjacent to the Patuxent River.

To test our predictions, we simulated both post-breeding public information and pre-breeding location cues at points located within the larger population of redstarts at our study site. The basic experimental design consisted of simulating post-breeding public information cues during the fledging period of one breeding season (to simulate successful territories) and then simulating pre-breeding location cues at a different set of locations during the arrival period the following year (to simulate the presence of territorial males). During the second year of the experiment, all points were monitored to determine the number of redstarts holding territories in the vicinity of each point. We repeated this design twice, with the first round initiated during the 2011 fledging period and completed during the 2012 arrival period (hereafter referred to as the 2012 round) and the second initiated in 2012 and completed in 2013 (hereafter referred to as the 2013 round).

In 2011 and then again in 2012, we selected points for our experiment and randomly assigned each point to one of three treatments: post-breeding public information ($n = 20$), pre-breeding location cues ($n = 20$) or control ($n = 30$). To minimize the influence of habitat structure or previous experience, we selected points that were similar in general habitat structure (e.g. forested) and we used point counts and territory surveys to ensure that all sites were ≥150m from existing redstart territories in the years of the experiment, though we were unable to determine whether sites had been occupied by redstarts in previous years. Additionally, all points were separated by >250 m. Playback treatments were not audible at distances greater than 100, so 250 m was adequate to ensure independence of experimental treatments.

For both the post-breeding public information and pre-breeding location cue treatments, playback was broadcast using a portable CD player (Supersonic SC251) housed in a waterproof box and connected to two speakers (Dual LU43PW) mounted 2 m above the ground, 20 m apart and facing in opposite directions. An automated timer (Borg General TA5027) turned on the playback each morning at 0500 and broadcast the treatment until 1400. Each song track was separated by 15 of silence and was alternated between the two speakers every 5 min to minimize habituation. Post-breeding public information treatments were broadcast during the local redstart fledging period (June 1-August 1) and consisted of locally recorded male and female redstarts vocalizing while feeding young and fledgling begging calls. Pre-breeding location cue treatments were broadcast during the arrival period at our study site (April 10-May 15) and consisted of locally recorded territorial male songs. In 2013, one pre-breeding location cue station failed and was removed from analysis, resulting in a total of 19 replications for this treatment. Because both anthropogenic and heterospecific cues can influence settlement patterns of birds, we chose not to apply any playback at control points (Betts *et al.* 2008).

To determine whether redstarts collect post-breeding public information by observing the reproductive performance of conspecifics (i.e. prospecting), we conducted 10-min point counts once per week during the public information treatment period at all post-breeding public information and control points. All point counts were conducted between 0600 and 1000 on days without rain or wind. After a 2-min settling period, any redstart seen or heard within 50 m of point during the 10-min point count was considered a prospector and we used a logistic regression to compare the number of prospectors at public information and control point. During the post-breeding period, the age and sex of redstarts with female-like plumage cannot be reliably determined (Pyle, Howell & Ruck 1997), so we did not record the age or sex of prospectors unless they were adult males.

During the 2012 and 2013 arrival periods, all treatment and control points were surveyed daily to record the presence of male redstarts. Any male that was observed within 75 m of a point on >3 consecutive days and responded aggressively to conspecific song was considered to be settled at that point.

MEASURING HABITAT STRUCTURE

Although treatment and control points were visually inspected to ensure similar habitat structure, fine-scale differences in habitat features could still have influenced settlement decisions. To control for the influence of habitat structure, we quantified vegetation features within a 5-m-radius circle centred on each point and within three more circles located 25 m from the centre at 0, 120 and 240° (Tarof, Ratcliffe & Grubb 2004). Within each circle, we measured five habitat features: the number of saplings [<3 cm diameter at breast height (DBH)], the number of trees (>3 cm DBH), the number of beech trees, the percentage shrub cover and the percentage canopy cover. For each tree, DBH was measured 2 m above the ground using a diameter tape. We chose to record the number of beech trees because this is the preferred nesting tree for redstarts at our study site (C. Rushing unpublished data) and therefore may influence settlement decisions. Shrub cover was visually estimated as the percentage of the ground covered in shrubs and was recorded on a scale of 1–4 (1 = 0–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%). To estimate percentage canopy cover, we photographed the canopy directly above each circle using a Nikon Coolpix 990 digital camera fitted with a Nikon LC-ER1 8 mm 180° fisheye converter and vertically mounted on a tripod. We then used Gap Light Analyzer 2·0 (Frazer, Canham & Lertzman 1999) to quantify the percentage canopy cover within each photograph. In addition to these five habitat features, we also estimated the mean tree basal area and the total basal area (TBA) within each circle. We calculated tree basal area as $0{\cdot}005454xDBH^2$ (James & Shugart 1970). To estimate TBA, we converted the tree basal areas to basal area/acre ($0ot00007854x$tree basal area) and then summed these measures for all trees within the circle (James & Shugart 1970).

For each habitat feature, measurements were averaged across the four circles to derive a single estimate for the entire point. A multivariate ANOVA indicated that the mean scores of the seven habitat variables did not systematically differ among the three treatments ($F_{14,122} = 1{\cdot}22, P = 0{\cdot}27$). To reduce the number of dimensions used to measure habitat structure, we then used a princile component analysis (PCA) to collapse our original seven variables into a smaller number of orthogonal predictors. The first two principle components described over half of the variation in habitat structure (see Supporting Information, Table S1), and we included these scores in our analysis of settlement at playback points (see below).

INFERRING DISPERSAL STATUS

To test our prediction about the influence of long-distance dispersal on the use of social information, we attempted to capture all males that responded to our experimental treatments and used stable hydrogen isotopes to determine the dispersal status of each individual. All individuals were captured in mist nets using decoys and playback of conspecific song. After capture, each individual was classified as either a yearling (1 year old) or an adult (>1 year old) following Pyle, Howell & Ruck (1997), fitted with an aluminium USFWS leg band and a unique combination of plastic colour bands, weighed to the nearest 0·1 g, measured for body size (bill length, bill width, bill depth, tarsus length and unflattened wing chord) to the nearest 0·5 mm and released.

During banding, we also collected one tail feather (R3) for stable hydrogen isotope analysis. Stable hydrogen isotopes in feather samples (δ^2H_f) vary geographically (Chamberlain *et al.* 1997; Hobson & Wassenaar 1997) and can be used to infer long-distance movements in birds (Wunder, 2010, 2012). Because redstarts grow tail feathers at their breeding location prior to fall migration, δ^2H_f values from redstarts that bred at our study site in 2011 and 2012 and were recaptured in 2012 and 2013 provided the expected δ^2H_f distributions for birds originating at our study site during the years of our experiment. We then used these distributions to probabilistically determine dispersal status of individuals captured at playback stations, with each individual classified as local or an immigrant based on a predefined threshold of correctly classifying local individuals (Van Wilgenburg *et al.* 2012). To determine whether our results were sensitive to the threshold used to classify dispersal status, we carried out our analyses using three progressively stringent thresholds (4 : 1 odds, 9 : 1 odds, 19 : 1 odds). See Appendix S2 for more details about stable isotope analysis and inferring dispersal status.

In addition to the individuals that responded to our experimental treatments, we also collected isotope data from 97 unbanded male redstarts (2012: $n = 62$, 2013: $n = 35$) in the general population at our study site. These data served as a baseline for comparing immigration patterns in our treatment groups.

ANALYSIS

Do social information and habitat structure influence settlement decisions?

To determine whether playback treatments and habitat characteristics influenced settlement decisions of redstarts, we tested whether the probability that sites settled by redstarts differed between treatments using a logistic regression model, which we refer to as the *settlement* model. Because we predicted *a priori* that settlement patterns would differ for adults and yearlings, we fit separate settlement models for each age class. For each age class, we modelled whether or not each site i was occupied by ≥1 redstart (denoted C_i) as a Bernoulli trial as follows:

$$C_i \sim \text{Bernoulli}(\psi_i) \qquad \text{eqn 1}$$

$$\begin{aligned} logit(\psi_i) = \alpha + \beta_1\text{Trt}_i + \beta_2\text{Year}_i + \beta_3\text{PC1}_i + \beta_4\text{PC2}_i \\ + \beta_5\text{PC1}_i * \text{Trt}_i + \beta_6\text{PC2}_i * \text{Trt}_i + \beta_7\text{Year}_t * \text{Trt}_i, \end{aligned} \qquad \text{eqn 2}$$

where ψ_i is the probability of settlement at site i, α is the baseline settlement probability at control sites, Trt_i is a dummy variables indicating whether site i received location cue treatment or post-breeding public information treatment, Year_i is a dummy variable indicating whether the treatment was applied in the second year of the experiment, and PC1_i and PC2_i are the first two habitat scores for site i. To test our predictions about the factors that influence breeding site selection of redstarts, we dropped each of the predictors from two and then tested the fit of the reduced model using a likelihood ratio test (LRT). For predictors that were included in significant interaction terms, main effects were tested by dropping both the main effect and interactions.

Does long-distance dispersal modify the use of social information?

Given the small sample size of our experiment, we used a simple Bayesian binomial model (Kéry 2010) to test whether individuals that settled at playback sites were more or less likely to be immigrants than individuals from the general population. We modelled dispersal by independently fitting binomial models for each of the treatment types and for the population as a whole. For each model, the parameter of interest was the probability that an immigrant settled a site. We also derived the posterior distribution for differences between the dispersal probability of each treatment and for the general population (denoted p_{diff}). For example, a positive p_{diff} indicated that individuals responding to playback were more likely to be immigrants than individuals from the general population and a negative value indicates that playback individuals were less likely to be immigrants. We evaluated the degree of overlap in 95% credible intervals for the estimates of p_{diff} to identify significant differences in immigration probability.

We estimated posterior probability distributions with MCMC algorithms in JAGS 3.4.0 (Plummer 2003) via the R2jags package (Su & Yajima 2014) in R v3.0.2 (R Core Team 2013). We used uninformative priors for all parameters: Normal (0, 100) for regression parameters in the settlement model and Uniform (0, 1) for parameters in the immigration model. Three chains were computed for each parameter, and we stored 25 000 samples from each chain after discarding the first 10 000 iterations as burn-in. Convergence of the chains was assured by visual inspection of trace plots and by Gelman diagnostics (Brooks & Gelman 1998). To assess model fit, we used posterior predictive checking (Kruschke 2010). For each model, we used draws from the posterior distribution of each parameter to simulate a data set of the same size as the observed data. We then plotted the simulated data against the observed data to graphically inspect the fit of each model (Appendix S3).

Results

THE USE OF SOCIAL INFORMATION BY AMERICAN REDSTARTS

Over the course of our experiment, 52·6% (10/19) of the sites receiving pre-breeding location cue treatments were settled by at least one adult redstart, compared to 10% (3/30) of the control sites and 0% (0/20) of the post-breeding public information sites. Model selection results indicated that adult settlement probability was positively influenced by location cue treatments and negatively influenced by habitat PC1 (Table 1). We found no evidence that year or habitat PC2 influenced settlement probability (Table 1) nor did we find evidence of an interaction between treatment and habitat (PC1: χ^2 = 2·2, d.f. = 2, P = 0·33; PC2: χ^2 = 0·05, d.f. = 2, P = 0·98). Therefore, our conclusions about adult settlement are based on the top model containing treatment effects and the main effect of habitat PC1. After controlling for the influence of habitat, the adult *settlement* model indicated that the probability of settlement at sites that received the pre-breeding location cue treatment was ~8× higher than at control sites (Table 2; Fig. 1). Model coefficients associated with the post-breeding public information treatment were not estimable because all sites that received this treatment were unoccupied by adults. Therefore, contrary to our prediction, we conclude that adults redstarts did not respond to these post-breeding public information treatments.

The top adult model also indicated that settlement probability was negatively associated with the habitat features associated with habitat PC1 (Table 2; Fig. 2). Factor loadings indicate that habitat PC1 was positively correlated with the number of trees and negatively correlated with shrub cover (Table S1), indicating that adult redstarts were more likely to settle at sites with few trees, and to a lesser extent high shrub cover. Although we did not find statistical evidence that treatment response of adults varied as a function of habitat, inspection of the treatment-specific habitat effects suggests that the strength of the habitat PC1 effect did differ among the three treatment levels but that we did not have sufficient power to detect this interaction (Fig. 2). Thus, it appears that habitat PC1 had a strong influence on which pre-breeding location cue sites were settled but only a weak influence at control sites and no influence at post-breeding public information sites. Furthermore, this result suggests that the settlement probability of adults at pre-breeding location cue sites was only higher than at control sites when these treatments were conducted at sites with low habitat PC1 scores.

Table 1. Factors influencing breeding site selection by American redstarts. Coefficient estimates (β) SE are from the settlement models for yearlings and adults. Because no adult males settled at points receiving the public information treatment, the public information coefficient was not estimable in the adult settlement model. χ^2, d.f. and P values for each predictor refer to the likelihood ratio test (LRT) used to compare the model without that predictor to the full model. The treatment predictor and year predictor treat control points and the year 2012 as dummy variables, respectively. Interaction terms from the full model that were not significant were dropped and are not displayed here. Bold values indicate predictor variables that were significant at the 0·05 level

Predictor	β	SE	χ^2	d.f.	P
Yearlings					
Intercept	−2·63	0·81	–	–	–
Treatment					
Public information	**0·38**	**0·91**	**11·4**	**2**	**0·003**
Location cues	**2·39**	**0·87**			
Year	−0·65	0·68	0·97	1	0·32
Habitat PC1	−0·26	0·23	1·35	1	0·24
Habitat PC2	**−0·65**	**0·29**	**5·87**	**1**	**0·02**
Adults					
Intercept	−3·24	1·07	–	–	–
Treatment					
Public information	–	–	**2·62**	**2**	<0·001
Location cues	**3·17**	**1·04**			
Year	−1·03	0·91	1·35	1	0·25
Habitat PC1	**−0·75**	**0·33**	**7·53**	**1**	**0·006**
Habitat PC2	−0·58	0·35	2·94	1	0·08

Table 2. Estimated odds ratios and 95% confidence intervals (CI) for parameters included in the top settlement models for yearlings and adults. For playback treatments, the odds ratio is the relative probability of settlement at sites receiving that treatment compared to the probability of settlement at control sites, after controlling for habitat features. Because no adult males settled at points receiving the public information treatment, the public information odds ratio was not estimable. For habitat effects, the odds ratio is the change in settlement probability associated with one unit change in the habitat score

Predictor	Odds ratio (e^{β})	2.5% CI	97.5% CI
Yearlings			
Control	–	–	–
Public information	1·19	0·23	6·93
Location cues	8·64	1·93	50·99
Habitat PC2	0·52	0·28	0·90
Adults			
Control	–	–	–
Public information	–	–	–
Location cues	11·51	3·12	10·56
Habitat PC1	0·55	0·28	0·91

For yearlings, 47·4% (9/19) of the sites receiving pre-breeding location cue treatments were settled by at least one adult redstart, compared to 10% (3/30) of the control sites and 20% (4/20) of the post-breeding public information sites. Model selection results indicated that yearling settlement probability was positively influenced by location cue treatments and negatively influenced by habitat PC2 (Table 1). We found no evidence that year or habitat PC1 influenced settlement probability (Table 1) nor did we find evidence of an interaction between treatment and habitat (PC1: χ^2 = 0·82, d.f. = 2, P = 0·66; PC2: χ^2 = 3·48, d.f. = 2, P = 0·18). Therefore, our conclusions

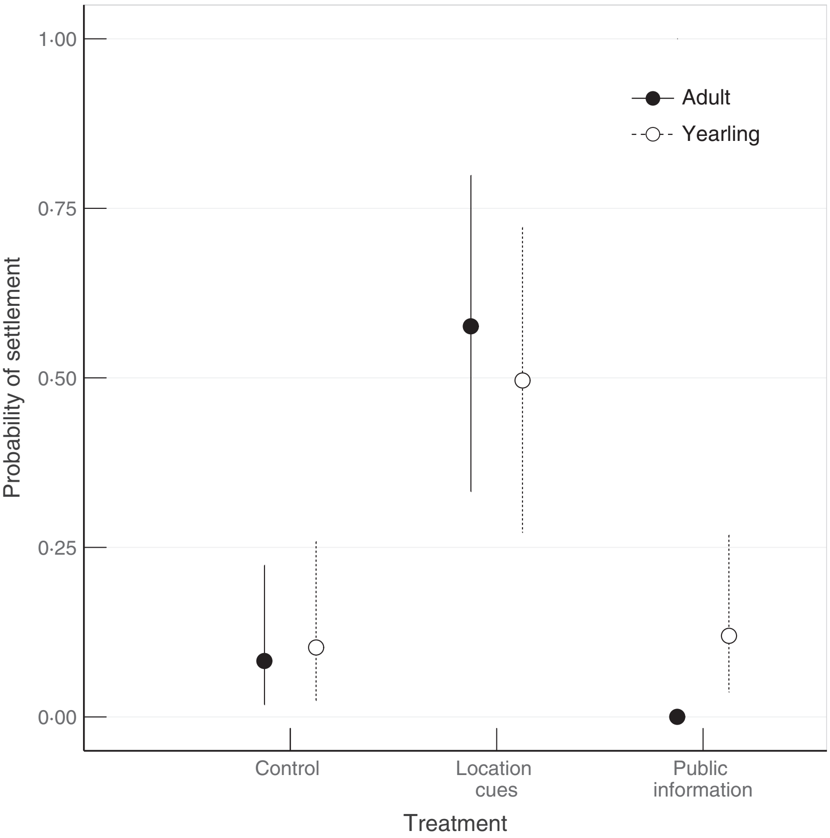

Fig. 1. Response of American redstarts to experimental playback treatments. Points show the predicted probability of settlement from the top *settlement* models for each age class, after controlling for the influence of habitat features. Error bars indicate the 95% confidence interval (CI) for each parameter. Model results indicate that, for both adults and yearlings, the probability of settlement at location cue points was significantly higher than at post-breeding public information or control points.

about yearling settlement are based on the top model containing treatment effects and the main effect of habitat PC2. After controlling for the influence of habitat, the yearling *settlement* model indicated that the probability of settlement at sites that received the pre-breeding location cue treatment was ~8× higher than at control sites (Table 2; Fig. 1). In contrast, the settlement model indicated the post-breeding public information treatment did not increase the odds of settlement compared to control sites (Table 2; Fig. 1).

As for adults, the top yearling model indicated that settlement probability was influenced by habitat features. However, unlike adults, yearling settlement was negatively associated with the habitat PC2 rather than PC1 (Table 1; Fig. 3). Habitat PC2 was positively correlated with the number of saplings and negatively correlated with mean tree basal area and percentage canopy cover (Table S1), indicating that yearlings chose sites that had higher tree basal area, and to a lesser extent higher percentage canopy cover and fewer saplings. Also as for adults, we did not find statistical evidence that treatment response of yearlings varied as a function of habitat but inspection of the treatment-specific habitat effects suggests that the strength of the habitat PC2 effect did differ among the three treatment levels (Fig. 3). In particular, it appears that that the influence of habitat PC2 on yearling settlement was stronger at sites that received playback treatments than at control points. Thus, although the settlement probability was always higher at location cue treatment sites than at public information treatment sites or control sites, this effect declined as habitat PC2 score increased. Furthermore, these results suggest that yearlings may have responded positively to post-breeding public information treatments, but only at sites with low habitat PC2 score. Unfortunately, although some of these sites were settled by yearlings, we were not able to conclusively attribute this response to our playback treatments.

EVIDENCE OF PROSPECTING

Over both years of the experiment, only two redstarts were recorded at post-breeding public information points during the playback period. The number of prospectors recorded at post-breeding public information points did not differ from the number recorded at control points ($n = 1$, $z = 0{\cdot}566$, d.f. = 1, $P = 0{\cdot}57$). Together with the settlement data, these results provide additional evidence that redstarts did not respond to our post-breeding public information treatments.

THE INFLUENCE OF LONG-DISTANCE DISPERSAL ON THE USE OF SOCIAL INFORMATION

Because we did not see a response to the post-breeding public information treatment, we restricted our analysis of long-distance dispersal to individuals that settled in response to pre-breeding location cues. The age ratio of yearlings to adults in the experimental group (1·5 year-

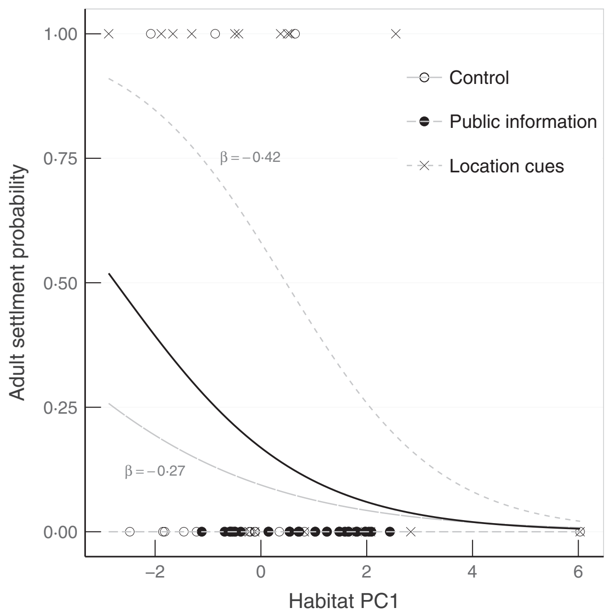

Fig. 2. Influence of habitat PC1 on the settlement probability of adult American redstarts. The solid line shows the estimated settlement probability from the top adult settlement model as a function of habitat PC1 for all points, independent of playback treatment. Dashed lines, and the associated slope coefficients, show the estimated effect of habitat PC1 for each treatment separately. Points show the observed settlement patterns within each treatment. Habitat PC1 was positively correlated with the number of trees and negatively correlated with shrub cover (Table S1), indicating that adult redstarts were more likely to settle at sites with few trees, and to a lesser extent high shrub cover. Although we did not find statistical support for a habitat × treatment interaction in the top model, treatment-specific habitat effects suggest that the effect of habitat PC1 may have been stronger at location cue treatments than at control sites or public information treatments.

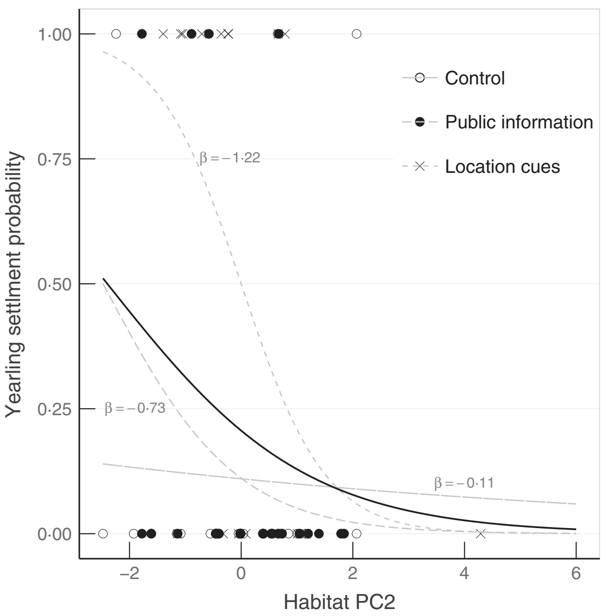

Fig. 3. Influence of habitat PC2 on the settlement probability of yearling American redstarts. The solid line shows the estimated settlement probability from the top yearling settlement model as a function of habitat PC2 for all points, independent of playback treatment. Dashed lines, and the associated slope coefficients, show the estimated effect of habitat PC2 for each treatment separately. Points show the observed settlement patterns within each treatment. Habitat PC2 was positively correlated with the number of saplings and negatively correlated with mean tree basal area and percentage canopy cover, indicating that yearlings responded more strongly to location cue treatments at sites that had higher tree basal area, and to a lesser extent higher percentage canopy cover and fewer saplings. Although we did not find statistical support for a habitat × treatment interaction in the top model, treatment-specific habitat effects suggest that the effect of habitat PC2 may have been stronger at playback sites than at control sites.

lings/adult) was similar to the age ratio of individuals sampled from the general population (1·42 yearlings/adult), allowing us to directly compare immigration rates without correcting for potential age-related biases. When immigrants were classified using a 4 : 1 odds ratio, the immigration rate for individuals that were captured at pre-breeding location cue points ($n = 15$) was significantly higher than the immigration rate in the general population ($n = 97$; $p_{\text{diff}} = 0{\cdot}22$, 95% CI = 0·007:0·46; Fig. 4). However, the immigration rates did not differ when dispersal status was classified using the more stringent 9 : 1 odds ratio ($p_{\text{diff}} = 0{\cdot}055$, 95% CI = −0·10 : 0·27) or the 19 : 1 odds ratio ($p_{\text{diff}} = -0{\cdot}02$, 95% CI = −0·12 : 0·13).

Discussion

At the beginning of the breeding season, male migratory birds are under severe time constraints to locate suitable habitat and establish territories. These tasks are made more challenging because the features that influence fitness (e.g. vegetation features, resource abundance, predation) are often not apparent at the time when settlement decisions are made. Under these circumstances, both pre-breeding location cues and post-breeding public information may provide reliable information for quickly locating suitable breeding sites but little is known about the relative importance of these cues in wild populations.

Our experimental simulation of pre-breeding location cues demonstrated that although both adult and yearling American redstarts use these cues to select breeding sites, the use of this information is modified by specific habitat features. For yearlings, response to location cues was strongest at sites with a high number of saplings and a low mean tree basal area. In contrast, settlement probability of yearlings at location cue sites did not differ from control sites in other habitat types. Likewise, adults responded strongly to location cue treatments at sites with more trees and lower shrub cover but settlement probability did not differ from control points in other habitat types. Unfortunately, we did have the necessary data to link these habitat features to reproductive performance so it remains unclear why the age classes used different habitat cues. However, it is worth noting that both the number and the size of trees are readily apparent at the

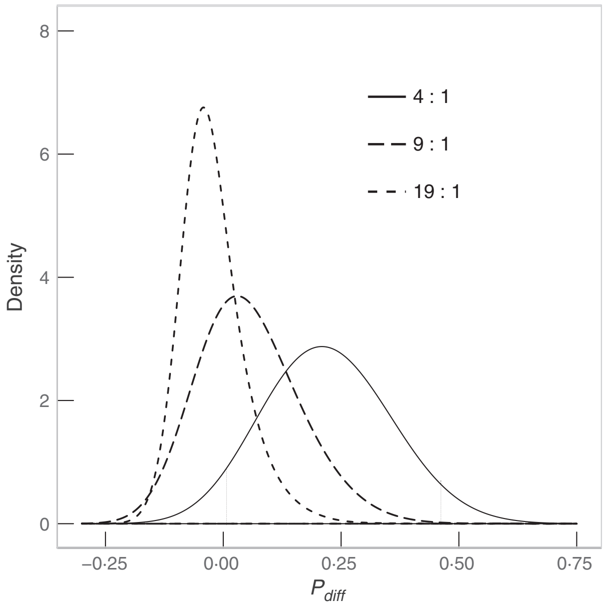

Fig. 4. Posterior distributions for difference in the immigration rate (p_{diff}) between individuals that settled in response to location cue treatments and individuals from the general population. When immigrants were classified using the 4 : 1 odds ratio, individuals that settled in response to experimental pre-breeding location cues were more likely to be immigrants than individuals in the general population and the 95% credible interval (CI), indicated by the vertical dotted lines, did not contain zero. However, immigration rates did not differ under the 9 : 1 odds ratio or the 19 : 1 odds ratio. The 95% CIs for the 9 : 1 and 19 : 1 odds ratio are not shown to reduce clutter.

beginning of the breeding season. If these features are indicative of habitat quality, using these habitat cues to modify the use of social information could provide an efficient and reliable method for selecting high-quality breeding sites. In particular, location cues could provide a rapid assessment of potential breeding locations (Stamps 1988). However, because these cues can become uncoupled from underlying habitat quality (i.e. ecological traps; Schlaepfer, Runge & Sherman 2002), modifying the use of this location cues based on easily assessed habitat features could provide a safeguard against settling in low-quality habitat (Szymkowiak 2013).

This strategy may be particularly important for individuals attempting to breed for the first time or in unfamiliar locations due to the lack of public information available to these individuals, a hypothesis which we were able to test using of stable hydrogen isotopes. When dispersal status was classified using a 4 : 1 odds ratio, our data indicate that the individuals that responded to pre-breeding location cue treatments were more likely to be immigrants than individuals from the general population. Furthermore, the immigration rate of the experimental group (35·3%) was high compared to immigration rates reported for other songbirds (e.g. Hansson *et al.* 2002; Abadi *et al.* 2010), including estimates based on hydrogen isotopes (Studds *et al.* 2012; Van Wilgenburg *et al.* 2012), suggesting that this group was disproportionately composed of long-distance dispersers. However, when dispersal status was classified using the more conservative 9 : 1 and 19 : 1 odds ratios, the immigration rate did not differ between pre-breeding location cue treatments and the general population. Thus, although our data provide some evidence that immigrants were more likely to use pre-breeding location cues, we were not able to conclusively accept or reject our prediction about the role of dispersal.

The inconclusive results of our dispersal analysis are likely related to several limitations of our methods that have made it difficult for us to detect an effect of dispersal on the use of social information. First, the geographic resolution of stable isotopes is low, and therefore, many of the individuals that were classified as local may have been short-distance dispersers that were using pre-breeding location cues. Secondly, although stringent thresholds (e.g. 9 : 1 and 19 : 1) make it less likely that local individuals will be misclassified as dispersers, increasing the threshold also makes the groups appear more similar, since a larger proportion of individuals in both groups will be classified as local. As a result, even if the immigration rates in the experimental group and general population differed, the more stringent thresholds may have falsely indicated that the two groups were similar. Finally, the general population almost certainly contained individuals that used location cues to select breeding sites, adding to the difficultly of detecting differences from our experimental group. Ideally, the birds that responded to our location cue treatments would be compared to a true control group made up of individuals that used a different strategy for selecting breeding sites. Unfortunately, too few redstarts settled at our control or post-breeding public information points to make such a comparison. Given the large difference observed under the 4 : 1 odds ratio, and the limitations associated with the more stringent thresholds, we suggest that our data provide at least moderate support for the prediction that long-distance dispersers rely on pre-breeding locations cues to select breeding sites to a larger extent than philopatric individuals.

The positive response that we observed in yearlings towards pre-breeding location cues contrasts with earlier research on redstarts, which found that adults, but not yearlings, responded to this source of social information (Hahn & Silverman 2006). However, in that study, playback was broadcast on plots already occupied by redstarts, whereas we purposefully placed our experimental treatments in locations that were uninhabited by redstarts. Yearling redstarts generally begin to arrive on the breeding around 7–10 days after adults (Hahn & Silverman 2006, C.S.R. Rushing *et al.* unpublished data) and are generally subordinate to adults when selecting breeding sites (Sherry & Holmes 1997). Therefore, the presence of early arriving adults on the plots used by Hahn & Silverman (2006) may have prevented yearlings from settling in response to their playback treatments. If competition for territories is responsible for the differences between our results and those of Hahn & Silverman (2006), than we would predict that sites in our experiment that were occupied by adults would be less likely to be occupied by yearlings. However, we found no relationship between adult occupancy and yearling occupancy ($\chi^2 = 2{\cdot}197$, d.f. = 1, $P = 0{\cdot}14$), suggesting that yearlings neither avoided nor were attracted to sites occupied by adults. This result may indicate that competition does not explain the discrepancy between our results and those of Hahn & Silverman (2006). On the contrary, our experimental design may have limited the severity of competition by purposefully selecting sites that were unoccupied by redstarts and thus reducing breeding densities. Given the age-specific influence of habitat cues observed in our experiment, it is also possible that the discrepancy observed between the two studies could have resulted from differences in the habitat types included in the experiments.

In contrast to the strong response to our location cue treatments, we found little evidence that redstarts use post-breeding public information to select breeding sites. No redstarts were observed prospecting at our public information treatments and, contrary to our prediction, no adult redstarts settled in response to public information treatments. Intriguingly, the response of yearlings to public information treatments appeared to increase in the same habitat types where we saw the strongest response to location cue treatments (Fig. 3), suggesting that some yearlings may have used post-breeding cues in preferred habitat types. Unfortunately, the large uncertainty in these responses did not allow us to conclusively determine whether settlement probability at these sites differed from settlement probability at control points with similar habitat features. Thus, although we were unable conclude that yearlings responded to our public information treatments, it is possible that subsequent experiments carried out in specific habitat types could find a response to these cues.

Several hypotheses could potentially explain the lack of response to our public information treatments. First, our treatments relied solely on auditory cues and the absence of visual cues (e.g. fledglings) could have kept redstarts from responding to our simulated cues. However, Betts *et al.* (2008) found that the closely related Black-throated Blue warbler responded equally to public information treatments with auditory cues only and to treatments with both auditory and visual cues. Because post-breeding song and fledgling begging calls are easily accessed by prospectors and are reliable indicators of reproductive performance, Betts *et al.* (2008) concluded that auditory cues alone are a sufficient source of public information for songbirds. Thus, the absence of visual cues is unlikely to explain the lack of response to our public information cues, though additional experiments are necessary to conclusively rule out this hypothesis.

A second explanation for the lack of response to public information treatments is that the single synchronous brood produced by redstarts limits the availability of post-breeding social information compared to species that have multiple broods per season. To date, most research on the use of public information has been carried out on colonial species (e.g. Aparicio, Bonal & Munoz 2007; Boulinier *et al.* 2008; Calabuig *et al.* 2008) or on species that breed asynchronously or produce multiple broods each year (e.g. Nocera, Forbes & Giraldeau 2006; Parejo *et al.* 2007; Betts *et al.* 2008). In contrast, relatively few experiments have tested whether public information is used in non-colonial, single-brooding species. Our results are in line with the those of Nocera, Forbes & Giraldeau (2006), who found that location cues were the primary source of social information for yearling bobolinks (*Dolichonyx oryzivorus*), another songbird with a short, synchronous breeding period. Thus, breeding synchrony and the number of broods produced within a breeding season may be important drivers of social information use, though additional experiments are needed to determine the generality of these conclusions.

Although the synchronous breeding season of redstarts may limit the availability of social information for young redstarts, 40–60% of yearling males in our population do not acquire a mate (C. Rushing, pers. obs.) and public information from the territories of successful adults should be available to these individuals (Doligez *et al.* 2004). The lack of response to post-breeding public information treatments by these individuals was particularly surprising given that the use of public information by non-breeding adults has been documented in a number of other migratory songbirds (Boulinier & Danchin 1997; Reed *et al.* 1999). The fact that they do not use this reliable source of information therefore appears to conflict with conventional research on the use of social information by migratory birds and suggests that breeding synchrony alone may not be sufficient to explain interspecific variation in the use of social information. Therefore, a third hypothesis for the lack of public information use by redstarts is that if selection favours a location/habitat cue strategy for first-time breeders and long-distance dispersers, there may be little need to develop an alternative public information-based strategy for future breeding attempts, particularly if individuals can supplement social information with personal information gained through reproductive experience. Unfortunately, it remains unknown whether this joint location/habitat cue strategy represents a viable alternative to the use of public information, largely because few studies have simultaneously compared the use of location cues and public information within the same species (Doligez *et al.* 2004; Nocera, Forbes & Giraldeau 2006) or directly tested how the use of social information is modified by biotic and abiotic conditions (Fletcher 2007; Betts *et al.* 2008). Furthermore, because many studies that fail to document behavioural responses to experimental treatments go unpublished (M. Betts, pers. comm.), generating and testing hypotheses about interspecific variation in the use of social information are difficult at present. Publication of negative results is critical to fully assessing when and why species use different types of social information, and we encourage researchers and publishers to make these results available.

Advancing this subject through experimental and comparative studies that explore the relationship between social information use, life-history traits and habitat quality is critical to predicting the vulnerability of species to changes caused by anthropogenic activities. Given that post-breeding public information is generally a reliable indication of breeding site quality, conventional wisdom holds that species that rely on public information should be less vulnerable to non-ideal habitat selection than species that rely on location cues (Doligez *et al.* 2003). Ironically, however, precisely because public information is reliable, species that rely heavily on public information may use these cues at the expense of directly assessing habitat features. Indeed, several studies on breeding site selection in migratory birds have found that experimental simulation of social information during the post-breeding period can trump habitat cues, leading individuals to settle in suboptimal habitat (Nocera, Forbes & Giraldeau 2006; Betts *et al.* 2008). For this reason, species that rely heavily on public information may be particularly vulnerable when anthropogenic activities make environmental conditions less predictable. In contrast, because the presence of conspecifics can more easily become decoupled from habitat quality (Schlaepfer, Runge & Sherman 2002), species that rely heavily on location cues may retain the ability to directly assess habitat quality as a safeguard against selecting unsuitable breeding sites (Szymkowiak 2013). If true, these species may be more resilient in the face of changing conditions than species that rely on public information.

Acknowledgements

All field methods were reviewed and approved by Animal Care and Use Committees at the Smithsonian Institution (#09-10), the University of Maryland (#325860-3) and the Patuxent Research Refuge (#NSR-NT-CT-0903). Access to the field site and logistical support was provided by the Patuxent Research Refuge. Two anonymous reviewers improved an earlier draft of this manuscript. The authors thank M. Betts and N. Rodenhouse for advice on assembling and operating playback stations. Funding for this project was provided by the Baltimore Birding Club's Dorothy Martin Memorial Fund, the Cosmos Foundation, the American Ornithologists Union and the Washington Biologists Field Club. The authors have no conflict of interests.

Data accessibility

Data available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.sf103 (Rushing *et al.* 2015).

References

Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R. & Schaub, M. (2010) Estimation of immigration rate using integrated population models. *Journal of Applied Ecology*, **47**, 393-400.

Ahlering, M.A. & Faaborg, J. (2006) Avian habitat management meets conspecific attraction: if you build it, will they come? *The Auk*, **123,** 301-312.

Ahlering, M.A., Johnson, D.H. & Faaborg, J. (2006) Conspecific attraction in a grassland bird, the Baird's Sparrow. *Journal of Field Ornithology*, **77**, 365-371.

Aparicio, J.M., Bonal, R. & Munoz, A. (2007) Experimental test on public information use in the colonial Lesser Kestrel. *Evolutionary Ecology*, **21**, 783-800.

Betts, M.G., Hadley, A.S., Rodenhouse, N. & Nocera, J.J. (2008) Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 2257-2263.

Betts, M.G., Nocera, J.J. & Hadley, A.S. (2010) Settlement in novel habitats induced by social information may disrupt community structure. *Condor*, **112**, 265-273.

Boulinier, T. & Danchin, E. (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology*, **11**, 505-517.

Boulinier, T., Mccoy, K.D., Yoccoz, N.G., Gasparini, J. & Tveraa, T. (2008) Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biology Letters*, **4**, 538-540.

Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7**, 434-455.

Calabuig, G., Ortego, J., Aparicio, J.M. & Cordero, P.J. (2008) Public information in selection of nesting colony by Lesser kestrels: which cues are used and when are they obtained? *Animal Behaviour,* **75,** 1611-1617.

Chamberlain, C., Blum, J., Holmes, R., Feng, X., Sherry, T. & Graves, G. (1997) The use of isotope tracers for identifying populations of migratory birds. *Oecologia*, **109**, 132-141.

Danchin, E., Giraldeau, L., Valone, T. & Wagner, R. (2004) Public information: from nosy neighbors to cultural evolution. *Science*, **305**, 487-491.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour*, **66**, 973-988.

Doligez, B., Part, T., Danchin, E., Clobert, J. & Gustafsson, L. (2004) Availability and use of public information and conspecific density for settlement decisions in the Collared flycatcher. *Journal of Animal Ecology*, **73**, 75-87.

Fletcher, R.J. (2007) Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology*, **76**, 598-606.

Fletcher, R.J. (2008) Social information and community dynamics: nontarget effects from simulating social cues for management. *Ecological Applications*, **18**, 1764-1773.

Frazer, G.W., Canham, C.D. & Lertzman, K.P. (1999) *Gap Light Analyzer (GLA), Version 2.0: Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-colour Fisheye Photographs*, Users Manual and Program Documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute for Ecosystem Studies. Millbrook, New York.

Fretwell, S.D. & Lucas, H.L. (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16-36.

Hahn, B.A. & Silverman, E.D. (2006) Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. *Biology Letters*, **2**, 337-340.

Hansson, B., Bensch, S., Hasselquist, D. & Nielsen, B. (2002) Restricted dispersal in a long distance migrant bird with patchy distribution, the Great reed warbler. *Oecologia*, **130**, 536-542.

Hobson, K.A. & Wassenaar, L.I. (1997) Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia*, **109**, 142-148.

James, F.C. & Shugart Jr, H.H. (1970) A quantitative method of habitat description. *Audubon Field Notes*, **24**, 727-736.

Kéry, M. (2010) *Introduction to WinBUGS for Ecologists: Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses*. Academic Press, Burlington, MA.

Kristan, W.B. (2003) The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos*, **103**, 457-468.

Kruschke, J. (2010) *Doing Bayesian Data Analysis: A Tutorial Introduction with R*. Academic Press, Burlington, MA.

Lovette, I.J., Pérez-Emán, J.L., Sullivan, J.P., Banks, R.C., Fiorentino, I., Córdoba-Córdoba, S., Echeverry-Galvis, M., Barker, F.K., Burns, K.J., Klicka, J. *et al.* (2010) A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). *Molecular Phylogenetics and Evolution*, **57**, 753-770.

Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1-13.

Nocera, J.J., Forbes, G.J. & Giraldeau, L.A. (2006) Inadvertent social information in breeding site selection of natal dispersing birds. *Biological Sciences*.**273**, 349-355.

Parejo, D., White, J., Clobert, J., Dreiss, A. & Danchin, E. (2007) Blue tits use fledgling quantity and quality as public information in breeding site choice. *Ecology*, **88**, 2373-2382.

Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. URL http://mcmc-jags.sourceforge.net/

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652-661.

Pyle, P., Howell, S.N. & Ruck, S. (1997) *Identification Guide to North American Birds: A Compendium of Information on Identifying, Ageing, and Sexing Waterbirds, Diurnal Raptors, and Gallinaceous Birds in the Hand. Anatidae to Alcidae*. Slate Creek Press, Bolinas, CA.

R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org

Reed, J.M., Boulinier, T., Danchin, E. & Oring, L.W. (1999) Informed Dispersal. *Current Ornithology*, **15**, 189-259.

Rushing, C.S., Dudash, M.R. & Marra, P.P. (2015) Data from: Habitat features and long-distance dispersal modify the use of social information by a long-distance migratory bird. *Dryad Digital Repository*. doi:10.5061/dryad.sf103.

Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. (2002) Ecological and evolutionary traps. *Trends in Ecology & Evolution*, **17**, 474-480.

Serrano, D., Forero, M.G., Donazar, J.A. & Tella, J.L. (2004) Dispersal and social attraction affect colony selection and dynamics of lesser kestrels. *Ecology*, **85**, 3438-3447.

Sherry, T.W. & Holmes, R.T. (1997) American redstart (*Setophaga ruticilla*). *The Birds of North America Online* (ed. A. Poole). Cornell Lab of Ornithology, Ithaca, NY.

Stamps, J. (1988) Conspecific attraction and aggregation in territorial species. *The American Naturalist*, **131**, 329-347.

Stamps, J. & Krishnan, V. (2005) Nonintuitive cue use in habitat selection. *Ecology*, **86**, 2860-2867.

Studds, C.E., McFarland, K.P., Aubry, Y., Rimmer, C.C., Hobson, K.A., Marra, P.P. & Wassenaar, L.I. (2012) Stable-hydrogen isotope measures of natal dispersal reflect observed population declines in a threatened migratory songbird. *Diversity and Distributions*, **18**, 919-930.

Su, Y.S. & Yajima, M. (2014) R2jags: A package for running jags from R. R package version 0.04-01.

Szostek, K.L., Schaub, M. & Becker, P.H. (2014) Immigrants are attracted by local pre-breeders and recruits in a seabird colony. *Journal of Animal Ecology*, 83, 1015-1024.

Szymkowiak, J. (2013) : How small songbirds acquire and use aocial information in habitat selection process?. *Springer Science Reviews* **1**, 115-131.

Tarof, S.A., Ratcliffe, L.M. & Grubb Jr, T. (2004) Habitat characteristics and nest predation do not explain clustered breeding in Least Flycatchers (*Empidonax minimus*). *The Auk*, **121**, 877-893.

Valone, T.J. (2007) From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioral Ecology and Sociobiology*, **62**, 1-14.

Van Wilgenburg, S.L., Hobson, K.A., Brewster, K.R. & Welker, J.M. (2012) Assessing dispersal in threatened migratory birds using stable hydrogen isotope (dD) analysis of feathers. *Endangered Species Research*, **16**, 17-29.

Ward, M.P. & Schlossberg, S. (2004) Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology*, **18**, 519-525.

Wunder, M.B. (2010) *Using Isoscapes to Model Probability Surfaces for Determining Geographic Origins*. pp. 251-270. Isoscapes, Springer, Dordrecht, the Netherlands.

Wunder, M.B. (2012) Determining geographic patterns of migration and dispersal using stable isotopes in keratins. *Journal of Mammalogy*, **93**, 360-367.

Received 23 February 2015; accepted 4 May 2015
Handling Editor: Michael Wunder

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Results of habitat principle component analysis.

Appendix S2. Additional information about stable isotope analysis and dispersal status determination.

Appendix S3. Posterior predictive checks for the settlement and dispersal models.

Appendix S4. R code used for analysis of playback and dispersal models.

Received Date : 28-Apr-2015

Revised Date : 10-Nov-2015

Accepted Date : 11-Nov-2015

Article type : Standard Paper

Editor: Gavin Siriwardena

Using demographic attributes from long-term monitoring data to delineate natural population structure

Clark S. Rushing[1,3], T. Brandt Ryder (RyderT@si.edu)[1], Amy L. Scarpignato (ScarpignatoA@si.edu)[1], James F. Saracco (JSaracco@birdpop.org)[2], Peter P. Marra (MarraP@si.edu)[1]

[1] Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington DC, USA

[2] Institute for Bird Populations, PO Box 1346, Point Reyes Station, CA 94956

[3] Corresponding author: MRC 5503 PO Box 37012, Washington, DC 20013
rushingc@si.edu, 404.295.9391 (c), 202-633-1237(f)

Running title: Delineating demographic population units

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2664.12579

Summary

1. The concept of “natural” populations is a foundation of modern ecology and conservation, with a large body of theoretical literature using these discrete demographic units to understand population dynamics and prioritize conservation strategies. To date, there are currently no objective methods for empirically delineating large-scale population boundaries using demographic data.

2. We present a novel approach for using large-scale, citizen-science monitoring data to quantify geographic structure in trend and abundance and identify distinct natural populations. We demonstrate this approach by delineating populations of eight passerine species using data collected as part of the North American Breeding Bird Survey.

3. Our approach was able to identify geographic structure in both trend and abundance and to delineate distinct populations for all eight species. An independent validation of three species indicated this demographic variation was reflected in underlying vital rates.

4. *Synthesis and applications.* Natural populations are biologically-based alternatives to the traditional geographically defined units that can improve the ability of researchers and managers to quantify spatial variation in population dynamics. Our analysis of natural population structure in breeding songbirds demonstrates that species can show substantial geographic variation in population attributes and underlying demography. We recommend managers define spatial units using natural populations when setting regional population objectives for both single and multi-species conservation plans.

Key-words: Andrewartha & Birch, Breeding Bird Survey, conservation planning, demography, hierarchical clustering, local population, monitoring, natural population, population dynamics

Introduction

In one of the seminal contributions to modern ecological theory, Andrewartha & Birch (1954) formalized the concept of ecological populations by recognizing that the dynamics shaping the distribution and abundance of species operate at two spatial scales: “local” populations and “natural” populations. At the local scale, immigration and emigration are the primary drivers of population dynamics, making local populations vulnerable to extinction/recolonization over short time-scales (Camus & Lima 2002). The local population concept has subsequently played a central role in modern population ecology and conservation by providing the foundation for metapopulation theory (Camus & Lima 2002). At larger spatial scales, however, immigration and emigration simply reshuffle individuals among local populations and therefore do not contribute to changes in the overall number of individuals over time. Thus, natural population (Andrewartha & Birch 1954) dynamics are governed primarily by birth and death processes rather than redistribution processes (Berryman 2002). On contemporary time-scales, natural populations form a fundamental unit for understanding ecological processes (i.e. spatial and temporal variation in demographic rates). Additionally, because natural populations act as distinct demographic units, they form the foundation for understanding the causes of species’ declines and for prioritizing conservation strategies (Hughes, Daily & Ehrlich 1997; Ceballos & Ehrlich 2002). However, despite the central importance of natural populations in ecology and conservation, objective methods to delineate demographic populations at large spatial scales remain unavailable (Camus & Lima 2002; Jones, Doran & Holmes 2007).

To date, the most progress on delineating large-scale population structure has occurred in the field of population genetics. Within the genetic population paradigm (Waples & Gaggiotti 2006), the processes that structure populations, such as mating, gene flow, and genetic drift, are well-studied (Slatkin 1987; Hartl *et al.* 1997) and researchers have developed a host of empirical approaches to delineate populations and identify genetic structure. For example, genetic markers (allele frequencies) and model-based clustering methods are often used to probabilistically assign individuals to populations or to define the number of genetically distinct populations in a host of vertebrate taxa (e.g. Falush, Stephens & Pritchard 2007). Likewise, the causes and consequences of genetic divergence have been used to define geographic structure in a number of animal taxa, including amphibians (Newman & Squire 2001), birds (Zink *et al.* 2000), and mammals (Rosenberg *et al.* 2002). These methods, combined with the large amount of published genetic and phenotypic data, have allowed researchers to make substantial progress in assessing the geographic structure of evolutionary processes and delineating genetic populations at appropriate biological scales. Although the methods available for delineating genetic populations are increasingly powerful, the results largely reflect the evolutionary population paradigm where populations are defined by the ability of individuals to mate or share genes (Waples & Gaggiotti 2006). In contrast, these approaches may not reflect the ecological population paradigm proposed by Andrewartha & Birch (1954), in which populations are defined by shared demographic rates (Waples & Gaggiotti 2006).

Unfortunately, there are currently no objective, quantitative approaches for using demographic data to delineate the boundaries of natural populations. Although some progress has been made in delineating demographic populations for species that occur in discrete breeding habitats (e.g. Ruckelshaus *et al.* 2006), most techniques currently used to delineate populations in ecological or management contexts are largely independent of the demographic processes that structure populations. Most commonly, populations are defined using study area borders (Berryman 2002), range limits (Ceballos & Ehrlich 2002), geographic isolation (Atwood 1991), or habitat limits (Sauer *et al.* 2003). Although these methods are undoubtedly useful in certain contexts (Vucetich, Nelson & Phillips 2006), they are largely arbitrary with regard to demographic processes and therefore provide little insight into the structure or scale of natural populations. Furthermore, because these methodologies do not account for the demographic attributes of populations that are most immediately relevant to conservation, management strategies often proceed in the absence of the critical information about demographic population structure (Rodrigues & Gaston 2002). Such shortcomings are likely to be most pronounced in species that inhabit large geographic areas that span political or habitat boundaries and display heterogeneous demographic trends across their range. Given the global decline of many such plant and animal species (Ceballos & Ehrlich 2002; Inger *et al.* 2015), there is a critical need for analytical methods that integrate demographic information to understand the geographic structure of natural populations.

In this paper, we develop an analytical approach that uses count data from a large-scale monitoring program to delineate natural populations. Our approach takes site-level estimates of trend and abundance and uses a spatially-explicit clustering technique to hierarchically group sites based on shared demographic attributes. The resulting cluster tree can then be used to determine the number of natural populations and delineate population boundaries. We use this approach to delineate the natural populations of eight species of breeding songbirds using data collected from the North American Breeding Bird Survey. To test whether our approach identified distinct populations, we used an independent demographic data set to test whether the trend and/or abundance differences among populations of three species were associated with differences in adult apparent survival and/or productivity. By quantifying spatial variation in demographic attributes (i.e. trend and abundance), our approach advances the natural population concept proposed by Andrewartha & Birch (1954) and provides a framework for understanding large-scale population processes and for conducting more efficient and effective conservation.

Materials and methods

Focal species and monitoring data

To develop our approach, we selected eight species of North American songbirds (four eastern and four western) that have been identified as conservation priorities based on either large range-wide declines or small geographic ranges (Table 1). The four species within each region were selected because they share similar habitat requirements, exhibit variation in breeding and non-breeding geographic range size, and display a variety of movement strategies (migratory vs. resident). Abundance data used for our analysis were obtained from the North American Breeding Bird Survey (BBS; https://www.pwrc.usgs.gov/bbs/RawData/), which provides reliable annual monitoring for all of the species included in our analysis.

We considered two time-scales for our analysis. First, we quantified contemporary population structure by limiting our analysis to BBS data collected between 2000 and 2013. Given that passerines have brief life spans and early sexual maturity, population dynamics operate over short time-scales (Sæther, Fallon & Johnson 2005) and therefore this recent period is expected to provide information about current demographic processes. Furthermore, because management efforts typically focus on contemporary rather than past threats, we also expect this time-scale to be of most immediate relevance to conservation and management. Because understanding how abundance changes over longer time-scales can be relevant to conservation, we also conducted a second analysis based on the full (1966–2013) BBS data. Here, we focus our analysis, results and discussion of population structure on the contemporary time-scale and use the long-term analysis as a means to quantify the degree to which geographic variation in trend and abundance contribute to the observed population structure.

Delineating populations

For each species, we first estimated the relative abundance and percentage annual change (i.e. trend) for each BBS route where the species was detected during the two periods. At each route, abundance was estimated as the mean of the annual counts, after correcting for route and observer effects (Link & Sauer 2002). Abundance estimates were then scaled to fall between 0 and 1 by dividing by the maximum abundance of each species. Route-level trends were estimated using a Poisson regression with the corrected annual counts as the response variable and year as a continuous predictor. See Appendix S1 for further details regarding estimation of route-level demographic rates.

Next, we used the trend, relative abundance, latitude, and longitude of each BBS route to calculate a multivariate Euclidean distance matrix for all routes for each of the eight species. Because the raw latitude and longitude values are numerically larger than the trend and abundance estimates, the multivariate distances were weighted by geographic distance. This weighting has the desirable property of ensuring that routes that are separated by large distances are less likely to be clustered together than routes that are close together and thereby provides a spatial constraint on population delineation. In contrast, we had no *a priori* reason to weight trend or abundance and since these attributes were similar in magnitude, we included the raw values in the distance matrix calculations.

For each species, the distance matrix was then used to perform a hierarchical agglomerative clustering analysis using the 'hclust' function in R (R Core Team, 2013) and Ward's method to estimate the distance between clusters (see Appendix S1). Hierarchical clustering begins with each of the n routes as a separate group and then uses the distance matrix to cluster routes, producing a hierarchical tree with $n - 1$ levels (Figures 1b & 2b). Once the BBS routes were clustered, the resulting hierarchical tree can be used to classify distinct geographic populations. To determine the number of populations for each of the eight species, we used the Kelley-Gardner-Sutcliffe (KGS) penalty function (Kelley, Gardner & Sutcliffe 1996) implemented using the 'kgs' function in the R package *maptree* v1.4-7 (White

& Gramacy 2012). The level of the tree with the minimum penalty represents the optimal number of groups (Carvalho *et al.* 2011; Appendix S1).

Although weighting geographic distance more heavily than demographic attributes is desirable for creating spatially-contiguous populations, one potential side effect is that the observed clustering structure may simply reflect geographic sampling location rather than variation in trend or abundance. We therefore used two methods to determine the degree to which population structure was influenced by the demographic data. First, we quantitatively assessed the relative contribution of the trend/abundance estimates to the observed clustering structure by comparing the topology of three trees built with identical geographic data, but different demographic data. The three trees used for this comparison were two demographic trees based on the contemporary (2000–2013) and long-term (1966–2013) BBS data plus a third tree based only on geographic distance between BBS routes (hereafter the 'geographic' tree). These comparisons are important because the geographic data in each tree are identical and as such any changes in topology are strictly the result of changes in the trend and/or abundance of BBS routes. We quantified changes in tree topology using the Robinson-Foulds distance metric (abbreviated *dT*; Robinson & Foulds 1981), which measures the number of internal branches found on one tree that are not found on the other (Kuhner & Felsenstein 1994). Because there is no direct statistical interpretation of *dT* values (Kuhner & Felsenstein 1994), we report all distances as a proportion of their theoretical maximum, which is $2n$-6 for two trees fit to the same *n* BBS routes. If clustering is driven solely by geographic distance, the trees will be identical and the *d*T value will equal 0. In contrast, *dT* values greater than 0 indicate that the inclusion or modification of trend/abundance data influenced tree topology.

We note, however, that because all three trees in our analysis use identical geographic data, the topologies will be correlated and the actual maximum will be less than the theoretical maximum. All *dT* values were estimated using the R package *phangorn* v1.99-13 (Schliep 2011).

Second, we used the KGS penalty method to compare the number of populations classified by each of the three trees and mapped their geographic boundaries to visually assess the role of trend/abundance data. If population structure is driven solely by geographic structure, we expected the three trees to produce the same number of populations and for population boundaries to remain unchanged when trend/abundance data are added or modified.

Assessing population structure

Once the structure and number of contemporary populations was determined for each species, we used five additional methods to assess the effectiveness of our method for delineating ecological populations. First, we used 'coef.hclust' function in the R package *cluster* to estimate the agglomerative/divisive coefficient for each species' tree (Maechler *et al.* 2014). The divisive coefficient varies between 0 and 1, with values close to 1 indicating that well-defined clusters have been identified. Second, we conducted a Non-Metric Multidimensional Scaling (NMDS) with the 'metaMDS' function in the R package *vegan* (Oksanen *et al.* 2014) to visualize the multivariate structure and place 95% confidence ellipses on the KGS defined populations. Third, we used the 'adonis' function in the R package *vegan* to examine the proportion of variance in the route-level trend and abundance distance matrices that was explained by the groupings from the KGS defined populations. Adonis is a permutation based

ANOVA that can partition variance explained in a distance matrix using pseudo *F*-statistics. Because the groupings implicitly account for spatial proximity, this method allowed us to examine the contribution of route-level trend and abundance after controlling for geographic proximity.

Fourth, we calculated population-level estimates of both trend and abundance and then tested whether each population differed significantly from adjacent populations in these attributes. For both metrics, we used a hierarchical model developed to estimate regional trends and abundances from BBS data (Link & Sauer 1998; 2002). For each population, we estimated abundance as the mean of the expected counts across years for all routes in the population. Trend was estimated as the geometric mean of the proportional changes in abundance (Link & Sauer 2002; Appendix S1). To determine whether adjacent populations differed in either trend or mean abundance, we derived posterior distributions for the difference in trend/abundance for all adjacent populations and considered any posterior with > 95% of the posterior density above or below zero to be evidence of significant differences in demographic attributes, though we also considered posteriors with > 90% of the density above or below zero as strong support for population differences.

Independent Validation of Population Structure

We independently validated the geographic structure of our contemporary natural populations using data from Monitoring Avian Productivity and Survivorship (MAPS) banding stations (DeSante, O'Grady & Pyle 1999) between 2000 and 2008 (data from years after 2008 were not available at the time of our analysis). Because MAPS stations do not sample canopy-dwelling species, we restricted our analysis to the three ground foraging species (Kentucky Warbler, Wood Thrush, and Eastern Towhee; Figure S1 in Supporting Information).

We assigned MAPS stations to population clusters by creating convex hulls around the BBS routes within each population and indexing each station by the population in which it is located. To assess variation in productivity among population clusters, we modelled the probability of a captured bird being a young bird as a logit-linear function of fixed population cluster effects and random station and year effects (see Appendix S1). We assessed variation in adult apparent survival probability among population clusters using ad hoc robust design Cormack-Jolly-Seber models (Hines, Kendall & Nichols 2003).

To validate the results of our clustering analysis, we first correlated the trend and abundance estimates for each population with the corresponding productivity and survival estimates. For each of the three species, if the trend or abundance estimates were strongly ($r \geq 0.7$) or moderately ($0.4 \leq r < 0.7$) correlated with the MAPS vital rates, we further tested whether adjacent populations that differed significantly in trend/abundance also differed with regards to productivity or survival. We did this by subsetting the MAPS stations to include only stations within the adjacent populations of interest and then fitting the productivity and survival models with and without population cluster as a fixed effect. The two models were then compared using a likelihood ratio test (LRT), with a significant LRT indicating that the populations differ with regards to the vital rate of interest. Because this test was carried out independently for each population pair, we applied a Bonferroni correction to each individual test to ensure that the overall Type I error rate did not exceed 0.05 for each species. Finally, for population pairs with significant LRT results, we checked whether the direction of the differences in productivity and/or survival were consistent with the differences in trend and/or abundance.

Results

Using the contemporary BBS data set, our method was able to delineate spatially-distinct populations that varied in both trend and abundance for each species (Figures 1, 2, S2–S8). On average, each species was divided into 13.25 populations (range 8–20; Table 2). When all eight species were considered, the number of populations was not significantly correlated with range size (Spearman's r = 0.486, *P* = 0.22). However, the number of populations was significantly correlated with range size when Western Wood-Pewee, the species with the largest range, was not considered (r = 0.941, *P* = 0.001). After accounting for range size, eastern species averaged more populations than western species (estimate ± SE= −7.03 ± 1.32, *P* = 0.006).

Comparisons of trees with different trend/abundance data indicate that variation in these attributes played a substantial role in shaping tree topology, and therefore population structure. When compared to trees built only with geographic data, the addition of contemporary trend/abundance data altered tree topologies by an average of 34% per species (range 23%–43%; Table 2). When the contemporary demographic trees were compared to the long-term demographic trees, tree topologies changed by an average of 29% per species (range 17%–40%; Table 2). Visual comparison of the population boundaries also indicated that adding or altering trend/abundance data had a large influence of the number and geographic configuration of populations (Figures S9–S10).

Across all eight species, the mean geographic area of the contemporary populations was 149 904 km^2 (Table 2). The geographic size of the populations was significantly correlated with the total geographic size of the breeding range (r = 0.966, $P < 0.001$), but did not differ between regions (estimate ± SE = -31890 ± 147700, $t = -2.16$, $P = 0.097$) or based on migratory status (estimate ± SE = -12640 ± 1.7780, $t = 3.94$, $P = 0.51$).

All four of our assessment methods indicated that the clustering analysis was able to identify and delineate regional populations that differed in demographic attributes. The agglomerative coefficients were > 0.99 for all species, indicating strong grouping structure for all eight species. Visual inspection of NDMS plots indicated that the groupings identified by the agglomerative clustering were largely distinct in ordination space (Figures S11–S12).

Results from the *adonis* models indicate that, for most species, the groupings identified by the agglomerative clustering explained a significant proportion of the variance in route-level trend and/or abundance (Table 2). For seven of the eight species, R^2 values for the variance in abundance explained by our groupings were significant at the $\alpha = 0.05$ level and all species had significant R^2 values at the $\alpha = 0.1$ level. R^2 values for the variance in trend explained by our groupings were significant at the $\alpha = 0.05$ level for half of the species (4/8) and were significant at the $\alpha = 0.1$ level for five of the eight species. For all eight species, the R^2 values were smaller for trend than abundance. Furthermore, all R^2 values were < 0.26, indicating that spatial constraints likely played a large role in grouping populations, especially for western species, which on average had lower R^2 values and dT values than eastern species.

Analysis of population-level trend and abundance provided strong evidence that our method was successful at identifying populations that were distinct with regards to trend and/or abundance (Tables S1–S8). Overall, 81% (135/166) of adjacent populations differed in trend and/or abundance with probability > 0.95 and 85% (142/166) differed with probability > 0.90. However, the proportion of populations that differed in demographic attributes was higher for eastern populations (92%; 112/122) than for western populations (68%; 30/44; $\chi^2 = 15.15$, $P < 0.001$). As with the results from the *adonis* models, this suggests that spatial constraints may have played a more important role in delineating populations of western species than of eastern species.

Overall, the comparison of vital rate estimates among adjacent populations provided independent support for the clustering results. For all three species with adequate MAPS sampling, trend estimates were moderately correlated with productivity estimates (Figure 3). The MAPS analysis also indicated that Eastern Towhee populations with higher productivity tended to have higher abundance ($r = 0.603$, $P = 0.013$). Comparison of productivity models with and without population as a fixed effect indicated that the vast majority of adjacent populations that differed significantly in trend also differed significantly in productivity, even after controlling for multiple comparisons (Wood Thrush: 88.2% (15/17) of population pairs; Kentucky Warbler: 100% (4/4) of population pairs; Eastern Towhee: 73.3% (11/15) of population pairs). Of the population pairs with significantly different productivity, the majority differed in the direction predicted based on their trend estimates (Wood Thrush: 93.3% (14/15); Kentucky Warbler: 100% (4/4); Eastern Towhee: 63.6% (7/11)). For Eastern Towhee, 93.3% (14/15) population pairs that differed significantly in abundance also differed in productivity and 64.3% (9/14) of those populations differed in the direction predicted based on the differences in abundance. No relationship was found between productivity and abundance in Wood Thrush ($r = 0.414$, $P = 0.21$) or Kentucky Warbler ($r = 0.16$, $P = 0.52$) populations and neither trend nor abundance was correlated with apparent survival for any of the three species.

Discussion

Ecologists have long acknowledged that advancing ecological theory and managing declining species requires an operational definition of what constitutes a population (Andrewartha & Birch 1954; Berryman 2002). Despite this recognition, there are surprisingly few methods available for quantifying geographic structure in demographic attributes and delineating ecological populations in an objective manner (Camus & Lima 2002). In this paper, we have proposed one such approach and demonstrate the application of our method using continental-scale count data for eight North American songbird species. For all eight species, our approach was able to identify geographic structure in trend and abundance and to delineate populations that show variation in these attributes. Comparisons of population structure across different periods and to purely geographic structure indicate that these patterns were shaped by spatial variation in population attributes and independent data collected via the MAPS banding program corroborate the regional demographic patterns obtained from the BBS data.

Pairwise comparison of adjacent population attributes confirmed that the vast majority (~85%) of adjacent populations differed significantly in either trend and/or abundance. In cases where adjacent populations did not differ in at least one attribute, visual inspection of the population maps suggest that spatial constraints may have been the primary cause of population delineation. For example, Kentucky Warbler populations 12 and 13 did not differ significantly in either trend or abundance (Table S3), but further inspection reveals that these populations share only a small portion of their borders (Figure S3). These spatial constraints appear to have been particularly important for western species, as indicated by the lower proportion of adjacent populations that differed in population attributes and the smaller *dT* values for the demographic vs. the geographic trees. The importance of spatial constraints for western species may result from the fact that these species occur in patchier habitats than the habitats used by the eastern species (Tewksbury, Hejl & Martin 1998).

Demographic data collected through the MAPS banding program provided an independent validation of the results obtained using BBS data. For the three species with adequate MAPS sampling, the demographic data provide evidence that the geographic structure in population trends was reflected in underlying vital rates, particularly productivity. Interestingly, productivity was positively correlated with trend for the two obligate long-distance migrants (Wood Thrush and Kentucky Warbler), but negatively correlated for the partial migrant/resident Eastern Towhee, possibly resulting from differences in density dependence between these migratory strategies (Both 2000). Productivity was also positively correlated with abundance for Eastern Towhees. In general, both abundance and productivity tended to be higher in southern populations than in northern populations (Figure S4), indicating that our clustering approach may have captured a latitudinal gradient in the number of broods per season (Greenlaw 1996). Assuming that abundance at BBS routes is an index of breeding density within each population, the lack of correlation between productivity and abundance in the two long-distance migrants again suggests that the abundance of obligate migrants and partial migrants may be controlled by different demographic factors. Alternatively, differences in abundance may be driven by variation in habitat quality, which may not be reflected in productivity rates if reproductive success is density-dependent. Regardless of the biological mechanisms, the MAPS data provide an independent validation that clustering local sites based on count data was able to quantify geographic structure in demographic rates. Furthermore, the scale of the populations identified by our approach is far larger than the typical dispersal distance of most songbirds (Tittler, Villard & Fahrig 2009), suggesting the movement dynamics likely played a negligible role in the observed geographic structure of these populations. As a result, the method we propose provides an operational approach that can link empirical studies to the theoretical framework proposed by Andrewartha & Birch (1954) over sixty years ago, explicitly linking local populations that share underlying vital rates.

Given the central importance of identifying demographic population structure to ecology and conservation, it is important that any approach for delineating populations is broadly applicable to many species. Conventionally, demographic rates have been collected by tracking individual organisms using labour-intensive and costly mark–recapture methods (White & Burnham 1999). Although these methods can provide reliable estimates of vital rates within the sampling area and time frame, implementing them over larger spatial and temporal scales is generally cost-prohibitive (Zipkin *et al.* 2014). As such, the scale of most vital rate data is of limited value for identifying range-wide population geographic structure. In contrast, count data are relatively easy to collect over large spatial and temporal scales and a large number of standardized monitoring programs already collect these types of data for many species (Smit, Zuiderwijk & Groenveld 1999; Weir & Mossman 2005; Roy, Rothery & Brereton 2007). Thus, the approach that we have outlined provides a robust and objective method for quantifying geographic structure in demographic attributes that is widely applicable to many existing monitoring programs. Furthermore, our approach could be refined to utilize less standardized types of count data, such as presence-only data or opportunistically collected citizen-science data. Given the growing number and availability of citizen-science data sets (Sullivan *et al.* 2009) and analytical tools to estimate demographic rates from these data (Zipkin *et al.* 2014), we expect that our approach will be applicable to a large number of plant and animal species.

Although assessing population structure is important to advancing ecological theory, we expect that our approach will be particularly valuable for scientists and managers tasked with mitigating the widespread declines observed in many species (Pimm *et al.* 2014). At present, conservation work is often conducted without regard to population structure (Hughes, Daily & Ehrlich 1997) or on populations that are delineated by geopolitical or geophysiographic boundaries (Vazquez, Rodriques & Arita 2008). Such arbitrary populations may not be useful for identifying the causal factors that are driving declines (Rodrigues & Gaston 2002) or for conservation of diversity at the population scale (Hughes, Daily & Ehrlich 1997). For example, bird conservation in North America is conducted within Bird Conservation Regions (BCRs) that share similar bird communities, habitat, and resource management issues (Commission for Environmental Cooperation, 1998). Although BCRs may be appropriate for regional coordination of bird conservation and management, it is unlikely their boundaries coincide with the boundaries of the natural populations of the species of concern. For the eight species included in our analysis, BCRs within each species range contained, on average, portions of 3.75 (± 0.97) different natural populations. This overlap indicates that each BCR contained, on average, only 26% of each natural population, underscoring the limitations of using BCR boundaries to assess demographic population structure.

In contrast to BCRs, our approach inherently captures the demographic and spatial attributes that are most directly relevant to population processes and subsequent conservation action. Moreover, our approach is scalable and can be tailored to match the temporal scale over which the ecological factors of interest operate. For example, comparing population structure across the contemporary and long-term data sets indicated that geographic patterns in trend and abundance have changed considerably for Kentucky Warblers and Wood Thrush, but have remained virtually unchanged for Hermit Warblers (Table 2). Additional comparisons of this nature could provide a powerful tool to understand how environmental factors have shaped contemporary population dynamics. Using our approach, it is also possible for managers to compare the tree topology and demographic population structure across multiple species, providing a rigorous method to quantify geographic regions that may be important for multi-species conservation planning.

Additionally, by combining monitoring data with information about population-specific abundance data, it may be possible to conduct viability analyses for each population and in this way determine the persistence of populations under future land-use and climate scenarios. For example, regional monitoring data within each population could be combined with remote-sensing data to quantify how land use and climate have influenced population dynamics. Moreover, by quantifying the drivers of population change within and among natural populations, conservation practitioners can differentiate and proactively manage for range-wide vs. region-specific threats and prioritize limited conservation resources among regions. The hierarchical nature of our classifications also allows managers to focus on more fine-scale geographic structure within regional populations to mitigate threats that are more local in nature. Regardless of how the population structure is used, our approach provides an alternative to using arbitrary boundaries to define populations and therefore increases the likelihood that population analyses will capture the underlying ecological dynamics that form the basis for conservation and management decisions.

Many conservation biologists argue that we have entered the sixth extinction characterized by the rapid decline of many populations (Hughes, Daily & Ehrlich 1997) and species (Pimm *et al.* 2014). Mitigating these declines will require the ability to delineate natural populations to understand the spatial scales at which demographic processes operate. Ecological dynamics do not take place in isolation from evolutionary dynamics or vice versa (Wiens & Graham 2005) and delineation of populations should ultimately account for both processes. As such, the development of effective conservation strategies in the face of rapidly changing global climate and land use will require the unification of the evolutionary and ecological population paradigms to consider both demographic vulnerability and genetic uniqueness (Crandall *et al.* 2000). Although both demographic and genetic data are rarely available for the same spatial and temporal scales, our approach could easily be expanded to incorporate both types of data to quantify biologically realistic population structure across space and time.

Acknowledgements

We thank S. Sillett, J. Hostetler, A-L. Harrison, T. Wilbert, G. Siriwardena, and three anonymous reviewers for comments that strengthened earlier drafts of this paper. CSR was supported by a Smithsonian James Smithson Postdoctoral fellowship. This work was made possible by the support from the Strategic Environmental Research and Defense Program and the U.S. Fish and Wildlife Service.

Data Accessibility

- Breeding Bird Survey: All BBS data used in this analysis are available at https://www.pwrc.usgs.gov/bbs/RawData/.
- Monitoring Avian Survival and Productivity: All MAPS data used in the analysis are available through the Smithsonian Digital Repository DOI: 10.5479/data.nzp.2015.1109 (Rushing *et al.* 2015).

References

Andrewartha, H.G. & Birch, L.C. (1954). *The distribution and abundance of animals.* University of Chicago Press.

Atwood, J. (1991). Subspecies limits and geographic patterns of morphological variation in California Gnatcatchers (*Polioptila californica*). *Bulletin of the Southern California Academy of Science*, **90**, 118–113.

Berryman, A.A. (2002). Population: a central concept for ecology? *Oikos*, **97**, 439–442.

Both, C. (2000). Density dependence of avian clutch size in resident and migrant species: is there a constraint on the predictability of competitor density? *Journal of Avian Biology*, **31**, 412–417.

Camus, P.A. & Lima, M. (2002). Populations, metapopulations, and the open-closed dilemma: the conflict between operational and natural population concepts. *Oikos*, **97**, 433–438.

Carvalho, J.C., Cardoso, P., Crespo, L.C., Henriques, S., Carvalho, R. & Gomes, P. (2011). Biogeographic patterns of spiders in coastal dunes along a gradient of mediterraneity. *Biodiversity and Conservation*, **20**, 873–894.

Ceballos, G. & Ehrlich, P.R. (2002). Mammal population losses and the extinction crisis. *Science*, **296**, 904–907.

Commission for Environmental Cooperation (1998). A proposed framework for delineating ecologically-based planning, implementation, and evaluation units for cooperative bird conservation in the U.S. Tech. rep., Commission for Environmental Cooperation, Montreal, Quebec, Canada.

Crandall, K.A., Bininda-Emonds, O.R., Mace, G.M. & Wayne, R.K. (2000). Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution*, **15**, 290–295.

DeSante, D.F., O'Grady, D.R. & Pyle, P. (1999). Measures of productivity and survival derived from standardized mist-netting are consistent with observed population changes. *Bird Study*, **46**, S178–S188.

DeSante, D. F., Saracco, J. F., Pyle, P., Kaschube, D. R., & Chambers, M. K. (2008). Integrating the MAPS program into Coordinated Bird Monitoring in the Northeast (US Fish and Wildlife Service Region 5). *The Institute for Bird Populations, Point Reyes Station, CA*.

Falush, D., Stephens, M. & Pritchard, J.K. (2007). Inference of population structure using multi-locus genotype data: dominant markers and null alleles. *Molecular Ecology Notes*, **7**, 574–578.

Greenlaw, J.S. (1996). *The Birds of North America Online*, Cornell Lab of Ornithology, Ithaca, NY, chap. Eastern Towhee (*Pipilo erythrophthalmus*).

Hartl, D.L., Clark, A.G. *et al.* (1997). *Principles of population genetics*. vol. 116. Sinauer associates Sunderland.

Hines, J.E., Kendall, W.L. & Nichols, J.D. (2003). On the use of the robust design with transient capture-recapture models. *The Auk*, **120**, 1151.

Hughes, J.B., Daily, G.C. & Ehrlich, P.R. (1997). Population diversity: its extent and extinction. *Science*, **278**, 689–692.

Inger, R., Gregory, R., Duffy, J.P., Stott, I., Voˇríšek, P. & Gaston, K.J. (2015). Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters*, **18**, 28–36.

Jones, J., Doran, P.J. & Holmes, R.T. (2007). Spatial scaling of avian population dynamics: population abundance, growth rate, and variability. *Ecology*, **88**, 2505–2515.

Kelley, L.A., Gardner, S.P. & Sutcliffe, M.J. (1996). An automated approach for clustering an ensemble of NMR-derived protein structures into conformationally related subfamilies. *Protein Engineering*, **9**, 1063–1065.

Kuhner, M. K., & Felsenstein, J. (1994). A simulation comparison of phylogeny algorithms under equal and unequal evolutionary rates. *Molecular Biology and Evolution*, **11**, 459-468.

Link, W.A. & Sauer, J.R. (1998). Estimating population change from count data: application to the North American Breeding Bird Survey. *Ecological Applications*, **8**, 258–268.

Link, W.A. & Sauer, J.R. (2002). A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology*, **83**, 2832–2840.

Maechler, M., Rousseeuw, P., Struyf, A., Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. (2014). *cluster: Cluster Analysis Basics and Extensions. R package version 1.15.2*.

Newman, R.A. & Squire, T. (2001). Microsatellite variation and fine scale population structure in the wood frog (*Rana sylvatica*). *Molecular Ecology*, **10**, 1087–1100.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2014). *vegan: Community Ecology Package. R package version 2.2-0*.

Pimm, S., Jenkins, C., Abell, R., Brooks, T., Gittleman, J., Joppa, L., Raven, P., Roberts, C. & Sexton, J. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**, 1246752.

R Core Team (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, D., & Foulds, L. R. (1981). Comparison of phylogenetic trees. *Mathematical Biosciences*, **53**, 131-147.

Rodrigues, A.S. & Gaston, K.J. (2002). Rarity and conservation planning across geopolitical units. *Conservation Biology*, **16**, 674–682.

Rosenberg, N.A., Pritchard, J.K., Weber, J.L., Cann, H.M., Kidd, K.K., Zhivotovsky, L.A. & Feldman, M.W. (2002). Genetic structure of human populations. *Science*, **298**, 2381–2385.

Roy, D., Rothery, P. & Brereton, T. (2007). Reduced-effort schemes for monitoring butterfly populations. *Journal of Applied Ecology*, **44**, 993–1000.

Ruckelshaus, M.H., Currens, K., Graeber, W., Fuerstenberg, R., Rawson, K., Sands, N. & Scott, J. (2006). Independent populations of chinook salmon in Puget sound. Tech. Rep. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-78, 125 p.

Rushing, C.R., Ryder, T.B, Scarpignato, A.L, Saracco, J.F, & Marra, P.P. (2015) Data from: Using demographic attributes from long-term monitoring data to delineate natural population structure. *Smithsonian Digital Repository:* https://repository.si.edu/handle/10088/27524.

Sæther, B.E., Lande, R., Engen, S., Weimerskirch, H., Lillegård, M., Altwegg, R., Becker, P.H., Bregnballe, T., Brommer, J.E., McCleery, R.H. *et al.* (2005). Generation time and temporal scaling of bird population dynamics. *Nature*, **436**, 99–102.

Saracco, J. F., Desante, D. F., & Kaschube, D. R. (2008). Assessing landbird monitoring programs and demographic causes of population trends. *The Journal of Wildlife Management*, **72**, 1665-1673.

Sauer, J.R., Fallon, J.E. & Johnson, R. (2003). Use of North American Breeding Bird Survey data to estimate population change for bird conservation regions. *The Journal of Wildlife Management*, **67**, 372–389.

Schliep K.P. 2011. phangorn: phylogenetic analysis in R. *Bioinformatics*, **27**, 592-593

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, **236**, 787–792.

Smit, G., Zuiderwijk, A. & Groenveld, A. (1999). A National Amphibian Monitoring Program in the Netherlands. *Current Studies in Herpetology*, pp. 397–402.

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S. (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, **142**, 2282–2292.

Tewksbury, J.J., Hejl, S.J. & Martin, T.E. (1998). Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology*, **79**, 2890–2903.

Tittler, R., Villard, M.A. & Fahrig, L. (2009). How far do songbirds disperse? *Ecography*, **32**, 1051–1061.

Vazquez, L.B., Rodríguez, P. & Arita, H.T. (2008). Conservation planning in a subdivided world. *Biodiversity and Conservation*, **17**, 1367–1377.

Vucetich, J.A., Nelson, M.P. & Phillips, M.K. (2006). The normative dimension and legal meaning of endangered and recovery in the US Endangered Species Act. *Conservation Biology*, **20**, 1383–1390.

Waples, R.S. & Gaggiotti, O. (2006). What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, **15**, 1419–1439.

Weir, L. & Mossman, M.J. (2005). *Amphibian Declines: conservation status of United States amphibians.*, University of California Press, chap. North American Amphibian Monitoring Pro- gram (NAAMP), pp. 307–313.

White, D. & Gramacy, R.B. (2012). *Maptree: Mapping, pruning, and graphing tree models. R package version 1.4-7.*

White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, S120–S139.

Wiens, J.J. & Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

Zink, R.M., Barrowclough, G.F., Atwood, J.L. & Blackwell-Rago, R.C. (2000). Genetics, taxonomy, and conservation of the threatened California gnatcatcher. *Conservation Biology*, **14**, 1394–1405.

Zipkin, E.F., Thorson, J.T., See, K., Lynch, H.J., Grant, E.H.C., Kanno, Y., Chandler, R.B., Letcher, B.H. & Royle, J.A. (2014). Modeling structured population dynamics using data from unmarked individuals. *Ecology*, **95**, 22–29.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Additional methods and materials.

Appendix S2: Additional summary figures and tables.

Table 1. Focal species summary: range-wide population statuses of the eight focal species included in our analysis. For trend estimates, values within parentheses are the 95% Bayesian credible interval

Species	Global population size[1]	Range-wide percentage annual decline[2]	Breeding range size (km^2)[3]	Long-distance migrant?
Eastern				
Wood Thrush* (*Hylocichla mustelina*)	11 000 000	-2.1 (-2.3, -2.0)	6 025 794	Y
Eastern Wood-Pewee (*Contopus virens*)	5 500 00	-1.4 (-1.6, -1.3)	7 070 129	Y
Kentucky Warbler* (*Geothlypis formosa*)	2 800 000	-1.1 (-1.5, -0.6)	3 035 602	Y
Eastern Towhee (*Pipilo erythrophthalmus*)	28 000 000	-1.4 (-1.6, -1.3)	5 303 850	N
Western				
Hermit Warbler* (*Setophaga occidentalis*)	2 500 000	-0.1 (-0.8, 0.6)	612 936	Y
Western Wood-Pewee (*Contopus sordidulus*)	9 200 000	-1.6 (-2.3, -1.1)	15 621 570	Y
Chestnut-backed Chickadee (*Poecile rufescens*)	9 700 000	-1.6 (-2.5, -0.7)	2 361 011	N
Black-throated Gray Warbler (*Setophaga nigrescens*)	2 400 000	-1.5 (-2.3, -0.7)	3 094 380	Y

[1] http://rmbo.org/pifdb/

[2] http://www.mbr-pwrc.usgs.gov/bbs/

[3] http://explorer.natureserve.org/

* Species included on the 2012 Partner's in Flight Watchlist

Table 2. Population grouping results: for each species, the number of demographic populations, as determined using the Kelley-Gardner-Sutcliffe (KGS) penalty function, mean population area, results of the *adonis* tests for trend and abundance (see text for details), and the Robinson-Foulds distance metric comparing the topology of the contemporary (2000–2013) hierarchical clustering tree to trees based on geographic distance only and on long-term (1966–2013) monitoring data

Species	**Number of populations**	**Mean population area (km^2)**	**Trend[1]**		**Abundance[1]**		**Robinson-Foulds Distance[2]**	
			R^2	***P***	**R^2**	***P***	**vs. geographic tree**	**vs. long-term tree**
Eastern								
Wood Thrush	17	187 036	0.017	0.048	0.26	< 0.001	0.36 (1128/3102)	0.35 (1100/3102)
Eastern Wood-Pewee	20	199 567	0.017	0.029	0.24	< 0.001	0.41 (1594/3738)	0.33 (1244/3738)
Kentucky Warbler	13	99 152	0.033	0.11	0.16	< 0.001	0.43 (468/1110)	0.40 (440/1110)
Eastern Towhee	17	175 161	0.077	<0.001	0.31	< 0.001	0.23 (676/2960)	0.21 (628/2960)
Western								
Hermit Warbler	8	18 350	0.10	0.099	0.11	0.089	0.36 (78/216)	0.17 (36/216)
Western Wood-Pewee	14	322 328	0.044	< 0.001	0.11	< 0.001	0.28 (495/1748)	0.28 (482/1748)
Chestnut-backed Chickadee	8	82 740	0.026	0.633	0.10	0.004	0.26 (102/394)	0.34 (134/394)
Black-throated Gray Warbler	9	114 901	0.028	0.58	0.12	< 0.001	0.39 (192/488)	0.37 (182/488)

[1] For trend and abundance, R^2 and *P*-values are based on the results of the *adonis* permutation test using the route-level trend/abundance matrix as the predictor and the population groupings as the fixed response variable.

[2] Robinson-Foulds distances (*dT*) are based on comparing the contemporary (2000–2013) demographic tree to either the geographic distance tree (left column) or the long-term (1966–2013) demographic tree (right column) and are expressed as the observed *dT* divided by the maximum possible *dT* (shown in parentheses).

Figures

Figure 1. Results of the population grouping for Wood Thrush. (a) Breeding range (in grey) and geographic structure of the 17 populations identified by clustering routes based on trend, abundance, and spatial proximity. Each point shows the location of Breeding Bird Survey routes that detected Wood Thrush between 2000 and 2013. (b) The hierarchical tree produced by the clustering algorithm. Nodes and branches are coloured based on population membership. (c) Population-level estimates of abundance (top) and trend (bottom) for each population. Bars show 95% Bayesian credible intervals.

Figure 2. Results of the population grouping for Hermit Warbler. (a) Breeding range (in grey) and geographic structure of the eight populations identified by clustering routes based on trend, abundance, and spatial proximity. Each point shows the location of Breeding Bird Survey routes that detected Hermit Warbler between 2000 and 2013. (b) The hierarchical tree produced by the clustering algorithm. Nodes and branches are coloured based on population membership. (c) Population-level estimates of abundance (top) and trend (bottom) for each population. Bars show 95% Bayesian credible intervals.

Figure 3. Correlation between trend estimates based on Breeding Bird Survey data and productivity estimates based on Monitoring Avian Productivity and Survivorship data for populations of three North American bird species. Note different axis limits on each plot.

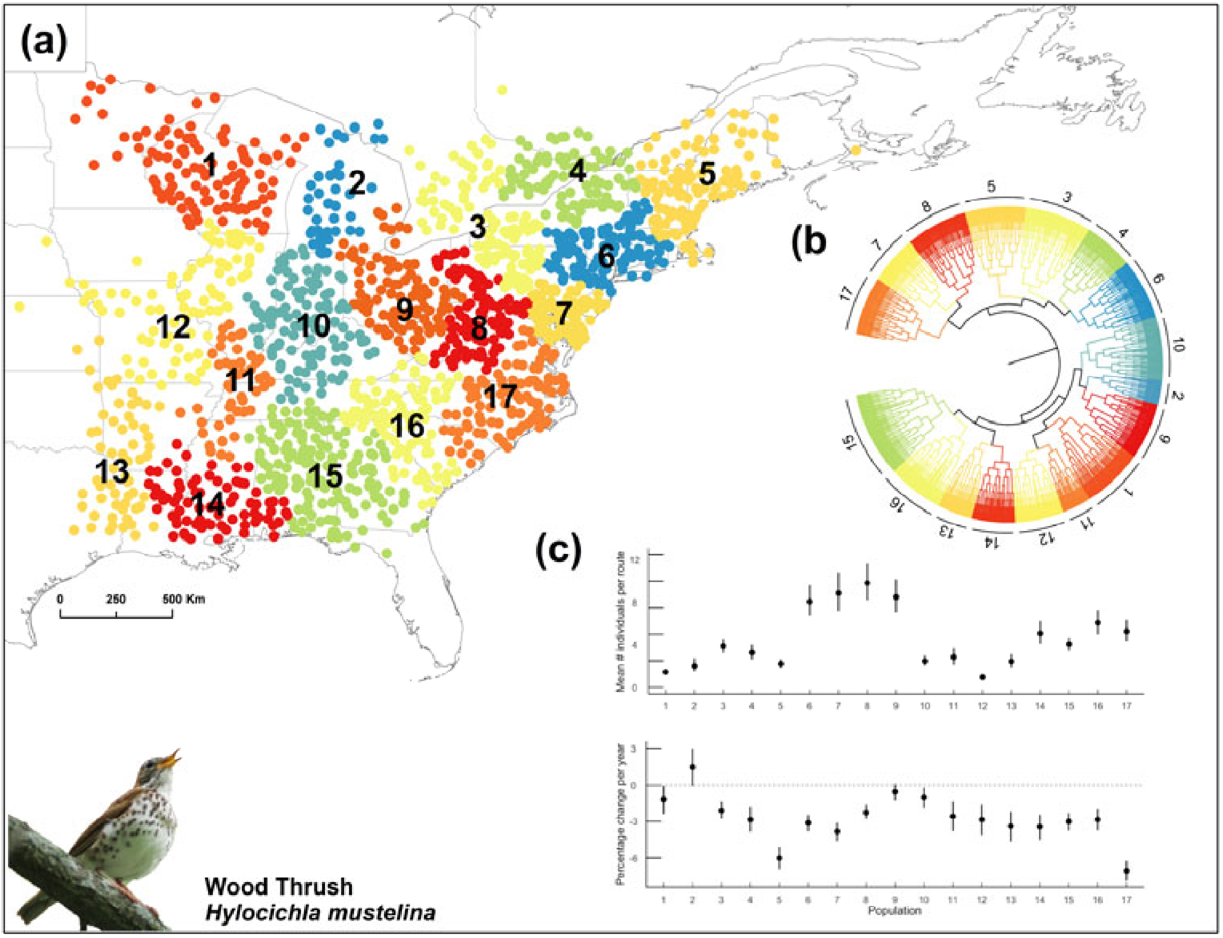
(a)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
0
250
500 Km
(b
5
3
4
6
10
2
9
1
11
12
14
13
16
15
17
7
8
(c)
Mean # individuals per route
12
8
4
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Percentage change per year
3
0
-3
-6
Population
Wood Thrush
Hylocichla mustelina

Figure 1

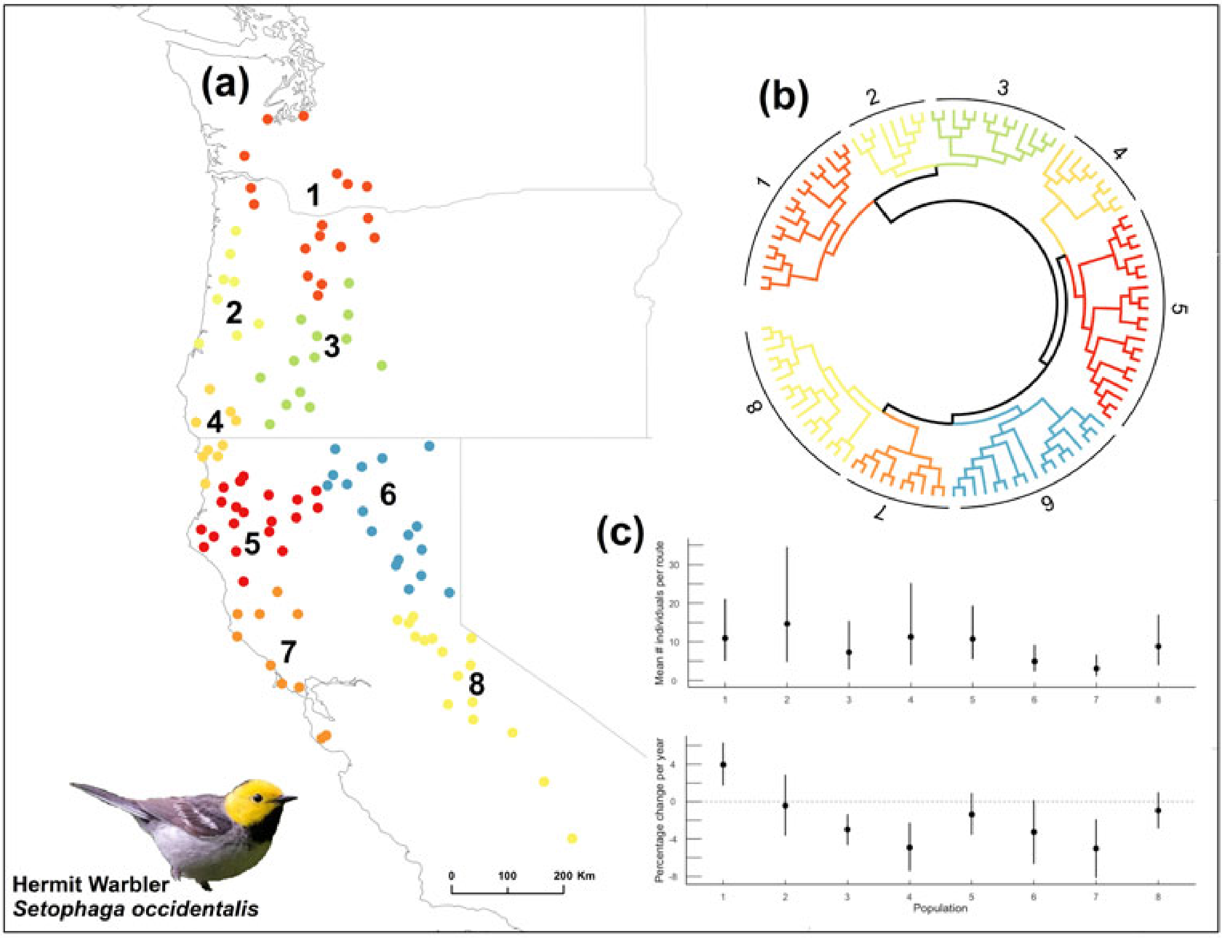
(a)
1
2
3
4
5
6
7
8
Hermit Warbler
Setophaga occidentalis
0
100
200 Km
(b)
1
2
3
4
5
6
7
8
(c)
Mean # individuals per route
30
20
10
0
1
2
3
4
5
6
7
8
Percentage change per year
4
0
-4
-8
1
2
3
4
5
6
7
8
Population

Figure 2

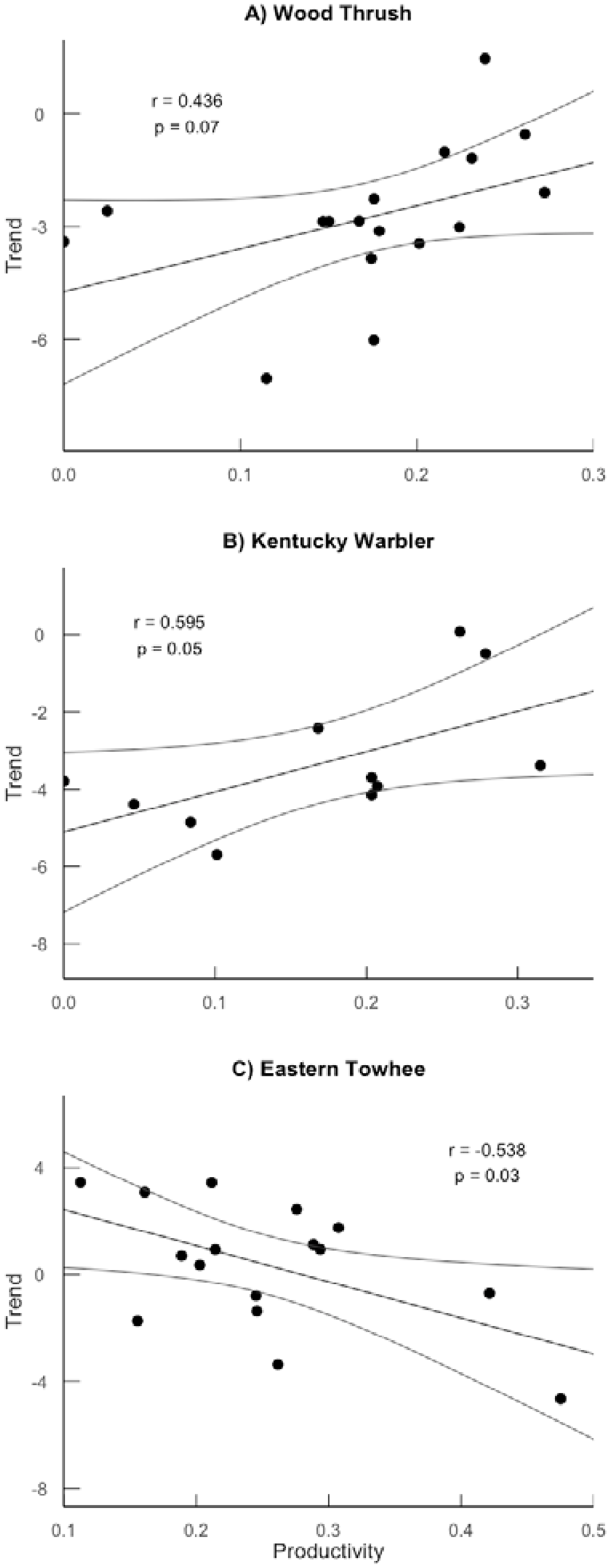
A) Wood Thrush
r = 0.436
p = 0.07
Trend
0
-3
-6
0.0
0.1
0.2
0.3
B) Kentucky Warbler
r = 0.595
p = 0.05
Trend
0
-2
-4
-6
-8
0.0
0.1
0.2
0.3
C) Eastern Towhee
r = -0.538
p = 0.03
Trend
4
0
-4
-8
0.1
0.2
0.3
0.4
0.5
Productivity

Figure 3