Integrated Analysis of Genetic, Stable Isotope, and Banding Data Reveal Migratory Connectivity and Flyways in the Northern Yellow Warbler (Dendroica petechia; aestiva Group)

Authors: Boulet, Marylène, Department of Biology, McMaster University, 1280 Main Street West, Hamilton, Ontario L8S 4K1, Canada, Gibbs, H. Lisle, Department of Biology, McMaster University, 1280 Main Street West, Hamilton, Ontario L8S 4K1, Canada, and Hobson, Keith A., Prairie and Northern Research Center, Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada

Source: Ornithological Monographs No. 61

Published By: American Ornithological Society

URL: https://doi.org/10.2307/40166837

Ornithological Monographs
Volume (2006), No. 61, 29–78

Printed in USA.

CHAPTER 2

INTEGRATED ANALYSIS OF GENETIC, STABLE ISOTOPE, AND BANDING DATA REVEAL MIGRATORY CONNECTIVITY AND FLYWAYS IN THE NORTHERN YELLOW WARBLER (*DENDROICA PETECHIA; AESTIVA* GROUP)

Marylène Boulet,[1,3] H. Lisle Gibbs,[1,4] and Keith A. Hobson[2]

[1]*Department of Biology, McMaster University, 1280 Main Street West, Hamilton, Ontario L8S 4K1, Canada;*
[2]*Prairie and Northern Research Center, Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada*

Abstract.—Population-specific genetic tags and stable isotope ratios are markers that can be used to track migratory birds throughout their annual cycle and determine their degree of migratory connectivity or the geographic linking of individuals or populations between different stages of the annual cycle. Until recently, few data had been obtained on the connectivity of small-bodied migrant birds such as warblers. Here, we combined geographic differences in mitochondrial DNA (mtDNA), stable hydrogen isotope (δD) analysis, and banding records to assess migratory connectivity in the northern yellow warbler (*Dendroica petechia; aestiva* group) populations and describe their migration patterns.

To use mtDNA variation to identify the geographic breeding region from which birds originated (eastern lineage: eastern and central North America; western lineage: western and central North America; southern lineage: southwest United States), we genotyped 133 wintering birds obtained from 23 sites in Mexico, Central America, and Venezuela; 438 spring migrants from 32 stopovers in North America; and 428 fall migrants from 30 stopovers in North America. There was strong segregation between lineages throughout the annual cycle: the eastern lineage was present in eastern and central North America during migration, and in Yucatan (Mexico), Panama, and Venezuela during the wintering season; the western lineage was present in central and western North America during migration and in Mexico and Panama during the wintering season; the southern lineage was restricted to western Mexico during the wintering season. The distributions of eastern and western lineages indicated strong continental-scale connectivity and a parallel migration system.

We conducted δD analysis on 94 feather samples collected from wintering birds captured on eight wintering areas and on 347 feather samples taken from migrants captured on six spring stopovers and five fall stopovers located in the United States and Mexico. For a large portion of these samples ($n = 407$), genotypic information was also available, and we combined these two types of information to create lineage-specific isotopic subregions to which birds were then assigned. The addition of the isotopic marker suggested weak connectivity between Mexican states along the Pacific coast and the west coast of North America, as well as between southeastern Mexican states along the Gulf Coast and central North America. Overall, the combined genetic and isotopic information identified the following migratory routes: in spring, there were three main flyways: a trans-Gulf route taken by eastern migrants passing through New York and Louisiana; a circum-Gulf route taken by eastern and western migrants passing through Veracruz, Mexico; and a western route taken by western birds passing through Nevada. In fall, there were two main flyways: the trans-Gulf route taken by eastern migrants passing through Alabama and the western–circum-Gulf routes taken by western migrants passing through California and possibly through New Mexico.

---

[3] Present address: Department of Biological Anthropology and Anatomy, Box 90383, 08 Bio Science Building, Duke University, Durham, North Carolina 27708, USA. E-mail: marylene.boulet@duke.edu

[4] Present address: Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 300 Aronoff Laboratory, 318 West 12th Avenue, Columbus, Ohio 43210, USA.

We obtained 6 banding records between breeding and wintering grounds and 46 banding records of migration movements through Canada and the United States, ranging from 1921 to 2002. For records between the breeding and wintering grounds, we recorded a wide diversity in breeding origins, providing independent support that Central America received migrants from a very wide array of breeding locales in North America. Mapping of migration movements suggested strong links between breeding grounds in eastern Canada and stopovers in the eastern United States; strong links between breeding grounds and stopovers along the Pacific coast from Alaska to California; and poorly defined links between breeding grounds and stopovers within central North America, concordant with patterns observed in the other markers.

In summary, the combined use of three types of markers provided sufficient resolution to detect general patterns of migratory connectivity in a widely distributed species. In terms of conservation, the finding of a parallel migration system suggests that migrant species with similar broad ranges could be managed using "phylogeographic flyways" to define demographically cohesive management units. *Received 14 November 2005, accepted 7 July 2006.*

Resumen.—Los marcadores genéticos específicos de las poblaciones y la proporción de isótopos estables, son marcadores que puedes ser usados para rastrear a las aves migratorias a lo largo de su ciclo anual y así determinar el grado de conexión migratoria o la unión geográfica de los individuos o poblaciones entre las diferentes etapas de su ciclo anual. Recientemente se han obtenido datos sobre la conexión de aves migratorias de talla pequeña como lo son las aves pertenecientes a la familia Parulidae. Aquí, combinamos las diferencias geográficas en ADN mitocondrial (ADNmt), análisis de isótopos estables de hidrogeno (δD) y registros de anillamiento para evaluar la conexión migratoria en las poblaciones de la subespecie *Dendroica petechia aestiva* y describimos sus patrones de migración.

Para identificar la región geográfica reproductiva de la cual las aves se originaron (linaje oriental: este y centro de América del Norte; linaje occidental: oeste y centro de América del Norte; linaje sureño: suroeste de Estados Unidos) mediante el uso de ADNmt, se obtuvieron los genotipos de 133 aves en invernada en 23 sitios en México, América Central y Venezuela; así como los genotipos de 438 aves migratorias en primavera de 32 áreas de descanso en América del Norte y los genotipos de 428 aves migratorias en otoño de 30 sitios de descanso en América del Norte. Existió una fuerte segregación entre los diferentes linajes a lo largo del ciclo anual: el linaje oriental estuvo presente en el este y centro de América del Norte durante la migración y en Yucatán (México), Panamá y Venezuela durante la temporada de invierno; el linaje occidental estuvo presente en el centro y oeste de América del Norte durante la migración y en México y Panamá durante la temporada de invierno; el linaje sureño estuvo restringido al oeste de México durante la temporada de invierno. La distribución de los linajes orientales y occidentales indicó una fuerte conectividad a nivel continental y un sistema migratorio paralelo.

Realizamos análisis de isótopos estables (δD) en 94 plumas colectadas en aves en invernada capturadas en ocho sitios de invernada y en 347 plumas colectadas de aves migratorias capturadas en seis sitios de descanso durante la primavera y cinco sitios de descanso localizados en los Estados Unidos y México. Existió información genotípica disponible para una gran parte de estas muestras (n = 407), y combinamos estos dos tipos de información para crear subregiones isotópicas especificas de los linajes a los cuales las aves fueron asignadas. La adición de marcadores isotópicos sugirieron una conexión débil entre los estados Mexicanos a lo largo de la costa del Pacifico y la costa oeste de América del Norte, así como también entre los estados del sureste de México a lo largo de la costa del Golfo y el centro de América del Norte. En general, la combinación de información de isótopos y genotipos pudieron identificarse las siguientes rutas migratorias: en primavera, hubieron tres rutas principales: la ruta trans-Golfo utilizada por aves migratorias del este pasando por Nueva York y Louisiana; una ruta circum-Golfo utilizada por aves migratorias del este y oeste pasando por Veracruz, México; y una ruta occidental utilizada por aves migratorias del oeste pasando por Nevada. En el otoño, se observaron dos rutas principales: la ruta trans-Golfo usada por aves migratorias del este pasando por Alabama y la ruta circum-Golfo occidental usada por aves migratorias del oeste pasando por California y probablemente por Nuevo México.

Obtuvimos 6 registros de anillamiento entre los sitios de reproducción e invernada y 46 registros de anillamiento de movimientos migratorios en Canadá y Estados Unidos, entre los años 1921 al 2002. Para los registros entre los sitios de invernada y reproducción, registramos una amplia diversidad en cuanto al origen de reproducción, dando un apoyo independiente a que América Central recibió aves migratorias proveniente s de una gran variedad de sitios de reproducción en América del Norte. Los mapas de los movimientos migratorios sugirió fuertes enlaces entre los sitios de reproducción en el este de Canadá y los sitios de descanso en el este de los Estados Unidos; así como fuertes enlaces entre los sitios de reproducción y sitios de descanso a lo largo de la costa del Pacífico desde Alaska hasta California; y enlaces poco definidos entre los sitios de reproducción y de descanso dentro de América del Norte, lo que concuerda con los patrones observados en los otros marcadores.

En resumen, el uso combinado de los tres tipos de marcadores ofreció suficiente resolución para detectar patrones generales de conexión migratoria en especies ampliamente distribuidas. En términos de conservación, el encontrar un sistema de migración paralela sugiere que las especies migratorias con rangos amplios similares podrían ser manejadas usando rutas de vuelo "filogeográficas" para definir unidades de manejo cohesivas demográficamente.

Effective conservation of migrant birds relies on our ability to understand interactions between all stages of their annual cycle (Esler 2000, Webster et al. 2002). This is because it is becoming increasingly apparent that all portions of the life cycle (the breeding season, fall migration, wintering season, and spring migration) are dynamically linked to each other (Hobson 2005, Webster and Marra 2005). For example, there is growing evidence that large-scale climatic events occurring at one stage of the cycle may have critical consequences on populations at subsequent stages (Peach et al. 1991, Sillet et al. 2000, Dugger et al. 2004, Norris et al. 2004). Similarly, winter habitat quality can affect individuals during the following breeding season. In Black-tailed Godwit (*Limosa limosa*), winter-site quality influenced winter survival, physiological condition, and timing of arrival on breeding grounds (Gill et al. 2001). In American Redstart (*Setophaga ruticilla*), males wintering in high-quality habitats arrived earlier on breeding grounds than males wintering in low-quality habitats (Marra et al. 1998), which likely increased their reproductive success (Møller 1994, Lozano et al. 1996, Hasselquist 1998). These results make it clear that we need to define the degree of demographic independence among migratory populations over the annual cycle (Esler 2000) and address significant questions, such as: Do populations that are segregated on the breeding grounds remain segregated on wintering grounds? Is there admixture on the wintering grounds and on stopovers?

Migratory connectivity is a concept that can be used to explore these questions. The term refers to the strength of association of individuals of a species during successive movements between breeding grounds, fall stopovers, wintering grounds, and spring stopovers (Webster et al. 2002, Webster and Marra 2005, Marra et al. 2006; but see Boulet and Norris 2006). Migratory connectivity is strong when most individuals from a given area migrate to a single area in the following period of the annual cycle, with only a small proportion of individuals of that population going to other areas. By contrast, there is no connectivity when individuals from a given area migrate equally to multiple areas the following season and mix with individuals from other populations (but see fig. 1 in Boulet and Norris 2006). Knowledge of patterns of connectivity can potentially be used to guide conservation actions for particular species. For example, in Swainson's Thrush (*Catharus ustulatus*), there is strong connectivity between breeding habitats along the Pacific coast in North America and wintering habitats in Central America, and between breeding habitats in eastern North America and wintering habitats in South America (Ruegg and Smith 2002). Consequently, if breeding populations along the Pacific coast show a sharp decline, then, to be effective, conservation efforts should target breeding habitats in western North America and wintering habitats in Central America, as well as the stopovers located between these two areas.

Migratory connectivity alone does not describe the mechanisms responsible for the distribution of breeding and wintering populations, or the migration system that generates the observed connectivity. Fifty years ago, Salomonsen (1955) reviewed the spatial segregation of wintering populations of numerous bird species throughout the world. Using morphological and plumage differences among subspecies combined with band-return data, he noted that some differentiated breeding populations mixed freely over the entire wintering grounds; that is, there was no connectivity (a synonym of synhiemy in Salomonsen's terminology), whereas in other species, differentiated breeding populations had distinct wintering grounds and, thus, showed strong connectivity (a synonym of allohiemy). Salomonsen defined four main types of migration systems that can produce strong connectivity: longitudinal, parallel, leap-frog, and cross-wise migration (see also Boulet and Norris 2006). Longitudinal migration describes populations that migrate along the same longitude but settle at different latitudes. Chain migration is an example of longitudinal migration. Parallel migration happens when two adjacent populations, breeding at the same latitude, migrate parallel to each other. Leap-frog migration occurs when populations occupying the northernmost breeding grounds winter on the southernmost wintering grounds, whereas those breeding farther south winter farther north. Finally, cross-wise migration describes cases where the migration routes of neighboring populations cross each other. Longitudinal and parallel migration systems are common, whereas leap-frog and cross-wise migration systems are rare (Salomonsen 1955). Although Salomonsen's review was extensive, it did not deal with bird groups that either had very low band-encounter rates or limited morphological differentiation. Until recently, assessing migratory connectivity and describing migration systems was particularly challenging in these groups. In North America, one such group includes Nearctic–Neotropical migrants, which generally breed in Canada and the United States and winter in Mexico, Central America, or South America. In Nearctic–Neotropical migrants, banding encounter rates <1% are typical (Brewer et al. 2000, Hobson 2003). This low success has led to efforts to find alternative techniques to document connectivity (Webster et al. 2002, Hobson 2005). In particular, much attention has focused on two methods: DNA-based genetic markers and stable isotope ratios.

Various types of genetic markers have been used with the goal of identifying genetic differences among breeding populations that could then be used to source wintering individuals. These include mitochondrial DNA (mtDNA; Wenink and Baker 1996, Wennerberg 2001, Kimura et al. 2002, Ruegg and Smith 2002), random amplified polymorphic DNA markers (RAPD; Haig et al. 1997), and DNA microsatellites (Clegg et al. 2003). For North America, mtDNA analyses have revealed a longitudinal divide between eastern and western populations that was concordant among a number of migrant species (Milot et al. 2000, Smith et al. 2005). However, because of the coarse resolution of the genetic differentiation, this type of marker has been useful only for detecting broad-scale connectivity among breeding and wintering grounds (Lovette et al. 2004). The recent postglaciation expansions in temperate-boreal species, high gene flow among populations, and retention of ancestral polymorphisms may obscure any finer phylogeographic structure (Bensch et al. 1999, Avise 2000, Milá et al. 2000, Bulgin et al. 2003). Nonetheless, differentiation at a continental scale offers an improved search tool for studying connectivity compared with what has previously been available (Kelly and Finch 1998, Webster et al. 2002).

Stable isotope techniques have been successfully used to link breeding and wintering populations in a range of birds (Hobson and Wassenaar 1997, 2001; Hobson et al. 2001; Meehan et al. 2001; Kelly et al. 2002; Rubenstein et al. 2002; Norris et al. 2006). A widely used isotope for this purpose is deuterium, a stable isotope of hydrogen. In North America, there is a continent-wide latitudinal pattern in stable hydrogen isotope ratios (δD, a measure of ^{2}H/^{1}H) in growing-season average precipitation that is transmitted through food webs (Hobson and Wassenaar 1997). When replacing feathers at the end of the breeding season, birds integrate the isotopic signature of the local environment into their new feathers, thus providing an approximate latitude-specific isotope tag. Stable hydrogen isotope variation across the continent has great potential for identifying molt- or breeding-site origins, especially when coupled with other stable isotopes, genetic markers, or band encounters (Caccamise et al. 2000, Rubenstein et al. 2002, Clegg et al. 2003, Lott et al. 2003, Smith et al. 2003, Kelly et al. 2005, Norris et al. 2006; but see Wunder et al. 2005). Use of both techniques is appealing because every individual captured and analyzed may carry genetic and isotopic information about the location of its breeding population, whereas more traditional techniques such as banding rely on the recapture of a small number of specifically marked individuals (Kelly and Finch 1998, Brewer et al. 2000, Hobson 2003).

As for most Nearctic–Neotropical migrants, little is known about migratory connectivity between populations of the northern yellow warbler (*Dendroica petechia; aestiva* group), the migratory form of the Yellow Warbler (*D. petechia*) that breeds in North America and winters from Mexico to South America. Most of the knowledge is based on the assignment of wintering individuals to one of the different subspecies with geographically distinct breeding ranges. For example, three subspecies from geographically widespread areas were identified as wintering in Veracruz, which suggests low connectivity between breeding and wintering populations in this area (Ramos and Warner 1980). Wintering ranges of subspecies tend to overlap, but there is also some evidence for segregation on the wintering grounds: boreal and eastern subspecies winter from eastern Mexico to northern South America, whereas Pacific coast subspecies winter from western and southern Mexico to northwestern South America (Bent 1963, Dunn and Garrett 1997). Regarding migration pathways, little is known about the routes used by specific breeding populations. The species distribution during migration indicates that northern yellow warblers may use any of the warbler migration routes, including (1) a Florida and West Indies route up to eastern North America; (2) a trans-Gulf route from the Yucatan Peninsula to the Gulf coast up to eastern North America; (3) a circum-Gulf route up to central North America; (4) a western route over the Rocky Mountains and Pacific coast; or (5) a Pacific route through Arizona and California (Dunn and Garrett 1997). During migration, banding encounters suggest that birds breeding from the Maritimes to the Prairies funnel through the eastern United States (Brewer et al. 2000). By contrast, descriptions of migration pathways used by subspecies suggest a possible parallel migration system among groups of subspecies (Bent 1963). Thus, there is a clear need for more analysis using additional tools that link breeding quarters, stopovers, and wintering quarters used by northern yellow warbler populations at finer scale than has been previously possible.

We have already identified three mtDNA lineages in this species: the eastern lineage breeding in eastern and central North America, the western lineage breeding in western and central North America, and the southern lineage breeding in the southwestern United States only (Milot et al. 2000, Boulet and Gibbs 2006). We showed that the distinct geographic distributions of these lineages can be explained primarily by historical isolation during Pleistocene glaciations and expansion after glacier retreat. Within the eastern and western lineages, gene flow was more important along the north–south migration axis than the east–west axis, which suggests that spring migration played a role in the dispersal of the lineages. Here, we assess migratory connectivity between breeding, wintering, and migrating populations of northern yellow warblers using data from mtDNA markers, stable hydrogen isotope analysis, and banding encounters. We begin by describing the annual distribution of these lineages. We then examine the following hypotheses about migratory behavior in these birds: (1) eastern and western mtDNA lineages will show strong longitudinal structure throughout the annual cycle (or strong migratory connectivity), as observed on the breeding grounds (Boulet and Gibbs 2006); (2) migratory connectivity will be very weak within each lineage, as suggested by the admixture of subspecies on the wintering grounds (Bent 1963, Ramos and Warner 1980); and (3) during migration, eastern and western lineages will stop at different stopovers and, thus, use different migration flyways because of their specific range distributions (Boulet and Gibbs 2006) and wind patterns (Gauthreaux 1980, Dunn and Garrett 1997). By contrast, within a lineage, breeding populations from distinct areas will use the same broad flyway on the basis of the observed admixtures of subspecies at stopovers and Canadian band returns (Raveling and Warner 1978, Brewer et al. 2000).

METHODS

STUDY SPECIES

Among wood warblers (Parulidae), the northern yellow warbler has the broadest breeding distribution, ranging from Alaska and Northwest Territories south to northern Mexico and from the Atlantic coast west to the Pacific coast (Appendix 1). The northern yellow warbler is the migratory form of the Yellow Warbler, a species that also includes two resident forms: the golden warbler (*D. petechia*; *petechia* group) from the West Indies and Florida, and the mangrove warbler (*D. petechia*; *erithachorides* group) from coastal Mexico, Central America, and northern South America. These resident taxa are genetically and morphologically distinct from the northern yellow warbler (Wiedenfeld 1991, Browning 1994, Klein and Brown 1994). The northern yellow warbler includes nine subspecies recognized on the basis of variation in plumage and morphology (Browning 1994).

Data Collection

To source wintering and migrant birds with respect to their breeding populations, we obtained samples from three types of tissues (feather quills, toe-pads, and blood) and three sources: birds captured in banding stations located in North America, museum specimens, and birds captured during field trips. Feather quills were obtained by pulling out two to four rectrices (from live animals) or one to two primaries (from museum specimens) and storing them in paper envelopes. Toe-pad samples were obtained from museum specimens by shaving tissues off the underside of two toes with a razor blade and then storing the sample in a plastic tube. Blood was sampled by puncturing the brachial vein, and a small quantity was then preserved in lysis buffer (Seutin et al. 1991). All sample types were stored at –20°C.

We obtained 684 samples from 56 breeding sites located in Canada and the United States (Appendix 2). Among these samples, 155 were from seven locales analyzed in a previous study (Milot et al. 2000). The geographic coordinates of the breeding sites ranged latitudinally from 35.2°N (Flagstaff, Arizona) to 64.8°N (Fairbanks, Alaska) and longitudinally from 57.7°W (Gros Morne National Park, Newfoundland) to 147.7°W (Fairbanks, Alaska). The geographic distribution of the sites covered most of the breeding range of this species, with fewer sites from the remote northern breeding areas. On the basis of the subspecies limits, our samples are from migratory subspecies breeding in North America and migrating to Mexico, Central America, or South America for the winter. The breeding status of most individuals was confirmed by the presence of well-developed sexual attributes (cloacal protuberance in males, brood patch in females), the observation of a territorial behavior, or the recapture of a returning breeder at the banding station site. When this information was lacking, we only used samples from individuals that had been captured during the breeding season of the specific capture area (end of May to end of July for most regions; see Lowther et al. 1999).

For wintering birds, we analyzed 133 samples obtained from 23 sites in Mexico, Belize, Panama, and Venezuela (Appendix 2). The majority of samples were collected in December to March over several years (1931, 1942, 1971, 1973–1975, 1980–1981, 1983–1984, 1993–1998, 2001–2002). Most samples (~75%) were collected after 1990.

To analyze samples from spring migrants, we used 438 samples from 32 spring stopovers located in Canada, the United States, and Mexico (Appendix 2). At banding stations, banders identified spring migrants by absence of cloacal protuberance or brood patch, absence of local bird band (i.e., not a returning and local after-hatch-year bird), date of capture (i.e., within the migration season: early April to early June, depending on the specific region; Dunn and Garrett 1997, Lowther et al. 1999) or high fat score. When this information was missing, we used the date of capture alone to determine whether birds were migrants according to migration dates reported in the literature (Lowther et al. 1999). In spite of these criteria, some early local males without cloacal protuberance could have been misidentified as migrants. However, migrants usually outnumber local breeders during migration, and this bias was likely negligible. Spring migrants were captured between early April and early June (earliest migrant caught in Louisiana on 7 April 2000 and latest migrant caught in Pennsylvania on 10 June 2001) during years 1961, 1975, 1998–1997, and 2000–2001. Most samples (97%) were collected after 1996.

Finally, samples from 428 fall migrants were obtained from 30 stopover sites in Canada, the United States, and Mexico (Appendix 2). Samples from museums were mostly from birds that died by hitting television towers during nocturnal migration. Fall migrants from banding stations were identified in the field by banders according to the following criteria: absence of molting feathers, absence of cloacal protuberance or brood patch, absence of a local bird band (i.e., not a local breeder or fledgling), and date of capture (i.e., within the migration season: mid-July to October according to regions; Lowther et al. 1999). Presence of furcular fat is another criterion used to identify a migrant, but the absence of fat is not an indication that a bird is not a migrant. When no other information was available, we compared the date of capture with published dates of migration for a particular region to classify individuals as migrants (Lowther et al. 1999). Migrants were collected between mid-July and the end of October (earliest migrant: 9 July 2000 in Pennsylvania; latest migrant: 29 October 1974 in Veracruz, Mexico) over several years (1961–1962, 1972–1974, 1992, 1994–2001), and the majority were collected over the last decade (88%: 1992–2002).

Mitochondrial DNA Analysis

We used a salt extraction protocol (L. DeSousa unpubl. data) to extract DNA from blood samples, and the QIAamp Tissue kit (Qiagen, Valencia, California) or the Genelute mammalian genomic DNA kit (Sigma-Aldrich, Oakville, Ontario) for the feather samples (see Boulet [2004] for additional details).

Northern yellow warblers are divided into three main mtDNA lineages: the eastern, western, and southern lineages (Boulet and Gibbs 2006). We used two methods to identify the mtDNA genotype of individuals: direct sequencing of a 333-base-pair (bp) control-region I (CRI) mtDNA fragment and lineage-specific polymerase chain reaction (PCR) amplifications of smaller mtDNA fragments that could discriminate western from eastern haplotypes. We sequenced 386 breeders, 129 wintering birds, and 31 migrants for phylogenetic analyses and verification of sequences found on the wintering sites and stopovers. We used the primers DPdl-L5 and DPdl-H4 (Milot et al. 2000) to amplify the 333-bp mtDNA CRI segment (see Boulet 2004). Some blood samples showed the presence of a co-amplified nuclear copy of the mtDNA segment ("numts"). To obtain clear and unambiguous sequences of the target mtDNA segment, we tested an alternative set of primers that amplified a 700-bp fragment, including the target fragment: ND6L303 (5′ C C/T AAC GAC ACC GAA TAA ACA AA 3′; H. L. Gibbs unpubl. data) and DLOOP-H700 (5′ TCA TGT GAT GGA CAT GTC AAG AGG 3′; H. L. Gibbs unpubl. data). We amplified this fragment in a 30-μL PCR reaction with 1 × PCR buffer, 170 μmol of dNTPs, 75 pmol $MgCl_2$, 0.5 U Taq polymerase (MBI-Fermentas, Burlington, Ontario), 50 ng DNA, and 130 pmol each of ND6L303 and DLOOP-H700. The reaction had 40 cycles of denaturation at 94°C (30 s), annealing at 55°C (30 s), extension at 72°C (45 s), with a final extension at 72°C (3 min). Tested samples had clear sequences with these primers and perfectly matched "clean" mtDNA haplotypes published by Milot et al. (2000). Samples were sequenced manually using the Thermosequenase kit (Amersham Biosciences [now part of GE Healthcare Life Sciences], Baie d'Urfé, Québec) or with an ABI3100 genetic analyzer (Applied Biosystem, Foster City, California) (see Boulet 2004).

To rapidly screen hundreds of individuals, we genotyped 298 additional breeders, 835 spring and fall migrant birds, and 4 wintering birds using lineage-specific primers that annealed to specific mutations: primer DPdl-EAST annealed to the eastern GCG motif and primer DPdl-WEST (5′TGG ACA TTC CTC GTT TGG 3′) annealed to the western CCA motif found at sites 234–236. We performed lineage-specific PCR reactions in a 10-μL reaction containing 1 μL of ancient DNA buffer, 300 μmol of dNTPs, 75 pmol $MgCl_2$, 0.2 U Taq polymerase (MBI-Fermentas), 50 ng DNA, and 100 pmol each of DPdl-EAST and DPdl-HS3 or DPdl-WEST and DPdl-HS3. Each reaction consisted of 35 cycles of denaturation at 94°C (30 s), annealing at 60°C (30 s), and extension at 72°C (45 s). We tested the accuracy of these primer pairs by amplifying individuals with 51 out of the 59 haplotypes identified by Milot et al. (2000). The primer pair DPdl-EAST and DPdl-HS3 amplified all eastern haplotypes (38 of 38) and 9 of 13 western haplotypes, whereas the primer pair DPdl-WEST and DPdl-HS3 did not amplify any of the eastern haplotype (0 of 38) and amplified all the western haplotypes (13 of 13). On the basis of these findings, we adopted the following protocol: we initially screened samples with DPdl-WEST and DPdl-HS3. Samples that showed a clear bright band on agarose gels were classified as western haplotypes, and samples that did not amplify were further tested using the DPdl-EAST primer. Samples that showed a clear bright band with DPdl-EAST and DPdl-HS3 were classified as eastern haplotypes. In every situation, we used a negative control and two positive controls (one known eastern haplotype and one known western haplotype). Samples that had weak and ambiguous band with both DPdl-EAST and DPdl-WEST primers were sequenced with DPdl-L5 and DPdl-H4 to determine their lineage. For example, birds of the southern lineage had a specific mutation at sites 234–236 (ACA) and were sequenced to identify their lineage (Appendix 2).

Geographic Distribution of Lineages

We used regressions to describe the geographic distribution of lineages at each season and determine whether lineages were longitudinally or latitudinally segregated (see Wennerberg [2001] for another example). For the breeding season, we used a multilogit model where the response categories were the eastern, western, and southern lineages (Proc LOGISTIC in SAS, version 8e [SAS Institute, Cary, North Carolina]; Agresti 1996). The reference category was the southern lineage. The model included the number of eastern, western, or southern haplotypes present within a given site and was weighted by the total number of haplotypes to account for unequal sampling among sites. For the winter, spring, and fall seasons, we did simple logistic regressions in Proc LOGISTIC because we had only two response categories, the eastern and western lineages. Southern haplotypes were excluded from these models because they were too rare ($n = 5$ on the wintering grounds and $n = 4$ during migration). The models were the number of eastern haplotypes present divided by the total number of samples within a given site. Differences in sampling size among sites could not be included in these specific logistic models. We used a stepwise procedure to identify significant variables of models (longitude, latitude, and the longitude*latitude interaction). We used Wald chi-square statistic to evaluate the unique significance of each variable. Presence of outliers in our data was detected by examining plots of observed versus predicted values, Pearson's chi-square and G^2 deviance residuals, and diagnostic measures of influence (Dfbeta, change in Pearson's chi-square and deviance G^2 goodness-of-fit statistics when an observation is deleted). In particular, large Pearson's residuals (less than –3 or >3) possibly influencing model fit were detected in Beatty, Nevada, in the fall; in Braddock, New York, Driftwood, Texas, and Inyo County, California, in the spring; and in central Oaxaca in the winter. These outlier values usually corresponded to a single eastern bird caught in the western part of the continent or a western bird caught in the eastern part of the continent. We suspect that these birds were long-distance dispersers or simply disoriented and, thus, had a biological relevance to the models. We kept these individuals in the analyses, but we evaluated the fit of the models using deviance G^2 statistics, which are less sensitive to departures when probabilities are very low ($P < 0.05$) or very high ($P > 0.95$) (Hosmer and Lemeshow 1989; but see Appendix 4). Models had high sensitivity and specificity (>85%) and explained at least 57% of the variation (see Appendix 4). For spring migration, we corrected for overdispersion in the spring data using the deviance option in Proc LOGISTIC. This option reduces the Wald chi-square values and increases P values and the confidence intervals of the estimated parameters. We also calculated the predicted probabilities of observing a specific mitochondrial lineage at a given site from the regressions (π_{east}, π_{west}, and π_{south}).

We then did a geostatistical analysis (kriging technique in the GEOSTATISTICAL ANALYST module of ARCGIS, version 8.0 [ESRI, Redlands, California]) on these predicted probabilities to globally describe the distributions of lineages in space (Bailey and Gatrell 1995, Johnston et al. 2001). We also did kriging analysis on the observed proportions of the lineages at each breeding site. However, the analysis was highly influenced by local variations in the proportions of eastern versus western lineages, especially in Michigan and Manitoba. We thus preferred using the predicted probabilities as opposed to the observed values to obtain contours that were less influenced by local variations and more representative of a broad regional pattern. Because this two-step method may introduce errors associated with the regression itself and the kriging routine, we carefully examined raw and predicted data versus the location of the contours. Details about the kriging technique are given in Appendix 5. We constructed three genetic contours (10%, 50%, and 90% probability) for the probability of observing each of the eastern, western, and southern mtDNA haplotypes (see Appendix 5 for details). The 10% contour delimited an exclusion zone where a lineage was absent and the 90% contour delimited an abundance zone where a lineage was extremely abundant. Thus, the area between the 10% and the 90% contours was defined as an overlap zone.

Migration Patterns of Lineages

To illustrate annual migration patterns in individuals belonging to the eastern and western mtDNA lineages, we summarized the four seasonal geographic distributions of haplotypes by computing a multivariate analysis of variance (MANOVA in Proc GLM). Dependent variables were the longitude and the latitude of sampling sites, and independent variables were season (breeding, fall migration, wintering, and spring migration), haplotype lineage and the season*haplotype interaction. We requested the least-square means statement with 95% confidence intervals and the slice option that tests for simple effects of a variable x for the variable y. We removed southern haplotypes from the analysis because they were too rare. We also excluded the few spring and fall stopovers located in Mexico, because this underrepresentation of southern sites with lowest latitudes could have biased the results (M. Boulet unpubl. data). The data set consisted of 674 individuals from 55 breeding sites, 414 individuals from 27 fall stopovers, 127 individuals from 21 wintering sites, and 379 individuals from 28 spring stopovers, for a total of 1,594 individuals.

An assumption of the MANOVA is the equivalence of the variance–covariance (VCV) matrices that can be tested with the Box's M test in SPSS, version 10.0 (SPSS, Chicago, Illinois). This test was highly significant, indicating that the VCV matrices were not homogenous. However, this test is overly sensitive to differences in matrices when the sample size is large (Norman and Streiner 2000). Log and square-root transformations of the raw data did not change the results of the Box's M test. Because we used the raw data (i.e., longitude and latitude) to make the results more interpretable (Norman and Streiner 2000), the results of the MANOVA should be interpreted with caution. We used Pillai's trace statistics for this test, because this statistic is more robust to violations of the MANOVA assumptions (Norman and Streiner 2000).

Connectivity Based on Stable Hydrogen Isotope Variation

Because they show latitudinal variation, δD values are best suited for identifying the broad latitudinal breeding area of wintering birds and migrants (i.e., whether birds are from a southerly or a northerly breeding region; Hobson and Wassenaar 1997). We analyzed 94 flight-feather samples (rectrices or primaries) taken from wintering individuals, 209 flight-feather samples from spring migrants, and 138 flight-feather samples from fall migrants, 408 of which were also genotyped. In spring, migrants were collected from 4 May to 9 June 2000 (36 days) in Beatty, Nevada; 4 May to 21 May 1998 (17 days) in Bosque del Apache, New Mexico; 6 May to 27 May 2000 (21 days) in Braddock Bay, New York; 13 April to 5 May 2000 (22 days) in Louisisana; 22 April to 16 May 1975 (25 days) in Los Tuxtlas, Mexico; and 19 April to 25 May 2001 (36 days) in Salinas, Mexico. In fall, migrants were collected from 27 August to 10 September 1998 (14 days) in Bosque del Apache, New Mexico; 2 September to 14 October 2000 (42 days) in Fort Morgan, Alabama; 4 September to 8 October 2000 (36 days) in Glenn and Tehama counties, California; on 7 September 1973, 7 October 1973, and 3 September 1974 to 2 November 1974 in Los Tuxtlas, Mexico; and on the night of 10 September 1962 in Westport, Minnesota. All migrants collected in the 1960s and 1970s were specimens housed at the Bell Museum, University of Minnesota in Minneapolis, whereas migrants sampled in 2000 and 2001 were collected during regular banding operations. Spring migration of northern yellow warblers is not consistent until mid-April and peaks in late April along the Gulf Coast. In New England, migrants arrive in mid-May and their numbers peak in late May, whereas in the western interior, migrants arrive in early May to mid-May. In the fall, the numbers of migrants peak along the Gulf Coast by mid-August to early September but some migrants persist through September and October. In the West, migrants are common by early August. They peak in late August and early September, but slightly later in coastal California. Moderate numbers of migrants are still observed in California in October (Dunn and Garrett 1997, Lowther et al. 2000). We selected these banding stations because they had the best coverage in terms of sampling days and number of birds. We may be missing early and late migrants in some collections (Bosque del Apache, New Mexico, in particular) if banding stations were not opened throughout all the northern yellow warbler migration seasons. Temporal patterns of migration at stopover sites are analyzed elsewhere (M. Boulet et al. unpubl. data; also see Boulet 2004).

Samples were processed by cleaning feathers in a 2:1 chloroform:methanol solution to remove surface contaminants and letting them air dry under a fumehood for several hours. Stable hydrogen isotope values were then determined for 55 samples using the offline steam equilibration method with dual-inlet stable hydrogen isotope (δD) analysis (Wassenaar and Hobson 2000, Hobson and Wassenaar 2001). This method provides δD measurements that are not influenced by uncontrolled hydrogen isotope exchange with ambient water vapor of the laboratory and yields isotopic values for the nonexchangeable hydrogen of tissues. The remaining samples (n = 387) were analyzed using a modification of the offline steam-equilibration technique: the comparative equilibration technique designed for continuous flow mass-spectrometric analyses using pyrolysis (Wassenaar and Hobson 2003). This latter method includes a comparative equilibration of samples with (offline) precalibrated keratin standards (chicken feathers, cow hoof, and bowhead baleen). Briefly, ~0.35 mg of feathers or powdered standards was wrapped in silver capsules. Samples were exposed to the ambient air of the laboratory at the National Water Research Institute (Saskatoon, Saskatchewan) for several days before analyses. We used a Eurovector 3000 high-temperature analyzer (Eurovector, Milan, Italy) to pyrolyse samples into a single pulse of H_2 gas at 1,270°C. A Eurovector GC column held at 100°C separated the H_2 pulse from N_2 and CO. The H_2 was then introduced to the isotope ratio mass spectrometer (Micromass Isoprime, GV Instruments, Manchester, United Kingdom). Finally, stable isotope ratios of feathers were corrected to the nonexchangeable component of feather hydrogen using a least-square regression of the precalibrated keratin standards. Standard deviation of the standard was ±2‰. However, Wassenaar and Hobson (2006) recently derived an expected upper limit of resolution for wild bird feathers of ±3‰ for deuterium measurements. For both techniques, δD values were reported as the nonexchangeable hydrogen fraction of feathers and were expressed in units per-mil (‰) relative to the VSMOW-SLAP (standard light Antarctic precipitation) scale. The two techniques are entirely comparable, because the standard aliquots were normalized with δD results obtained by analyzing standards of the same stock with the offline equilibration dual-inlet method (Wassenaar and Hobson 2003).

We used three types of tests to describe the structure of stable hydrogen data: variance component analyses to partition within-group and among-group sums of squares, permutation tests to compare δD mean values between lineages and between sites, and regressions to examine spatial patterns in δD values. Variance component analyses were performed in SPSS. We compared δD mean values among mtDNA lineages to determine whether lineages have, on average, distinct stable isotope signatures that would indicate use of distinct isotopic regions in North America. We also compared δD mean values among eight wintering areas to determine whether wintering areas are composed of the same pool of birds (i.e., whether there is evidence of segregation or not). We pooled all data within Mexican states to increase sampling size. We also examined δD mean values across eight stopovers sites sampled in 2000–2001 to identify sites with relatively similar mean δD values. Sites with similar δD mean values may be located along the same flyway because they receive the same pool of birds. For these tests, we ran the "comparisons of means test procedure" nested in PERM (Duchesne et al. 2006) and used 1,000 resampling events for each of the 10 iterations. This permutation procedure was specifically developed for stable isotope data. Probability (P) values were stable across iterations, which meant that we had run sufficient permutations per iteration. We adjusted P values of pairwise comparisons using sequential Bonferroni corrections (Rice 1989). Finally, we used linear and quadratic regressions weighted by sample size to test for longitudinal and latitudinal patterns in δD values of flight feathers collected on the eight wintering areas.

Individual Assignment Based on Stable Hydrogen Isotope and Genetic Contours

We used an analysis that combined isotopic and genetic information to assign wintering and migrant individuals to their likely breeding area in the following way. First, we modified the contour map of growing-season average precipitation δD values for

North America published by Hobson and Wassenaar (1997). Briefly, we included 11 additional sites from northern areas not used previously (International Atomic Energy Agency 2001). We added a correction factor of –25‰ to these precipitation values to account for isotopic fractionation between rainfall and passerine feathers (Wassenaar and Hobson 2001, Mazerolle and Hobson 2005). Because Hobson and Wassennar (1997) obtained a very tight relationship between δD of feathers from birds sampled at breeding locations and δD of the local growing-season average precipitation δD ($r = 0.91$), we also included 14 additional sites where δD values were obtained from Nearctic–Neotropical migrants caught on breeding grounds. This map has, thus, one of the best geographic coverages in North America (n = 62 sites). We used ordinary kriging in ARCGIS to produce a map of stable hydrogen contours (see details of this model in Appendix 5). We did not correct for altitudinal effects when building the stable hydrogen contours to use new data from northerly regions in our map. In addition, there were no qualitative differences between the two methods (K. A. Hobson unpubl. data). The use of a stable-hydrogen contours map is based on the assumption that long-term average δD values in rain falling at a given site during the growing season are reflective of the food-web water of this site for any given year. Ideally, migrants and wintering birds caught during a given year should be assigned to a breeding area using a stable isotope map derived from feathers collected the same year (for fall migrants and wintering birds) or the year before (for spring migrants). However, two papers have recently shown little effect of year of sampling on the relationship between derived precipitation δD values and measured feather δD values (Kelly et al. 2002, Lott and Smith 2006). Specifically, samples of Wilson's Warblers (*Wilsonia pusilla*) and raptors were obtained from museum collections throughout the past century and, in each case, year accounted for little of the total variance in feather δD values.

To assign birds to genetic and isotopic regions, we defined three isoclines that defined four large isotopic regions: (A) greater than –65‰, (B) –65‰ to –104.9‰, (C) –105‰ to 144.9‰, and (D) less than –145‰. The 40‰-wide intervals were ~4× the average standard errors of the stable-hydrogen kriging model. Then, we overlaid the 10% genetic contours obtained from the kriging analysis of predicted probabilities to the stable hydrogen contours to define source breeding regions. The addition of the 10% genetic contour restricted the isotopic regions to areas where the mitochondrial lineage was present (i.e., ≥10%) and created subregions specific to each lineage. For example, the region A-west includes individuals of the western lineage with a stable hydrogen value greater than –65‰. Finally, each individual captured on the wintering grounds or stopovers was assigned to a breeding subregion according to its lineage and feather isotopic value.

Banding Recapture Data

We obtained records of northern yellow warblers captured from 1921 to 2002 from the Bird Banding Office of the Canadian Wildlife Office in Ottawa. The data set contained location data (recorded in 10-min blocks) for all encounters for North and South America and is more complete than the data presented in the Canadian Atlas of Bird Banding (Brewer et al. 2000). We categorized encounters into two groups: direct encounters (i.e., encounters occurring during the same season of banding capture or during the season following the banding capture) and indirect encounters (i.e., recaptures occurring at least two seasons after the banding capture). Indirect encounters cannot be used to identify direct migration movements between two sites. However, they provide useful information to identify linkages between the sites used by an individual throughout its life cycle. Moreover, northern yellow warblers often return to the same breeding and wintering sites year after year (Lowther et al. 1999). We used the extension PATH WITH DISTANCES AND BEARINGS, version 3.0 (Jenness 2002), in ARCVIEW to calculate the distances between banding and encounter sites based on geodetic curves for increased accuracy. We excluded movements <200 km, leaving a total of 11 direct movements and 46 indirect movements that were then mapped.

Results

Mitochondrial DNA Lineage Distribution on Breeding Grounds

Overall, the three lineages had distinct geographic distributions on the breeding grounds. Eastern haplotypes were present from Newfoundland to Alberta in Canada and from Rhode Island to Montana in the United States, whereas western haplotypes were present from Manitoba to Alaska and from Michigan to California (Fig. 1). Southern haplotypes were restricted to the southwestern part of the breeding range: they were found in Lake Mead, Nevada (n = 6); Flagstaff, Arizona (n = 3); and Vernal, Utah (n = 1). The distributions of the lineages overlapped in the U.S. Central Great Plains and the Canadian Prairies (eastern and western lineages), as well as in the southwestern United States (southern and western lineages). There was no evidence of admixture between the eastern and southern lineages.

The spatial distributions of the three lineages were best explained by latitude, longitude, and

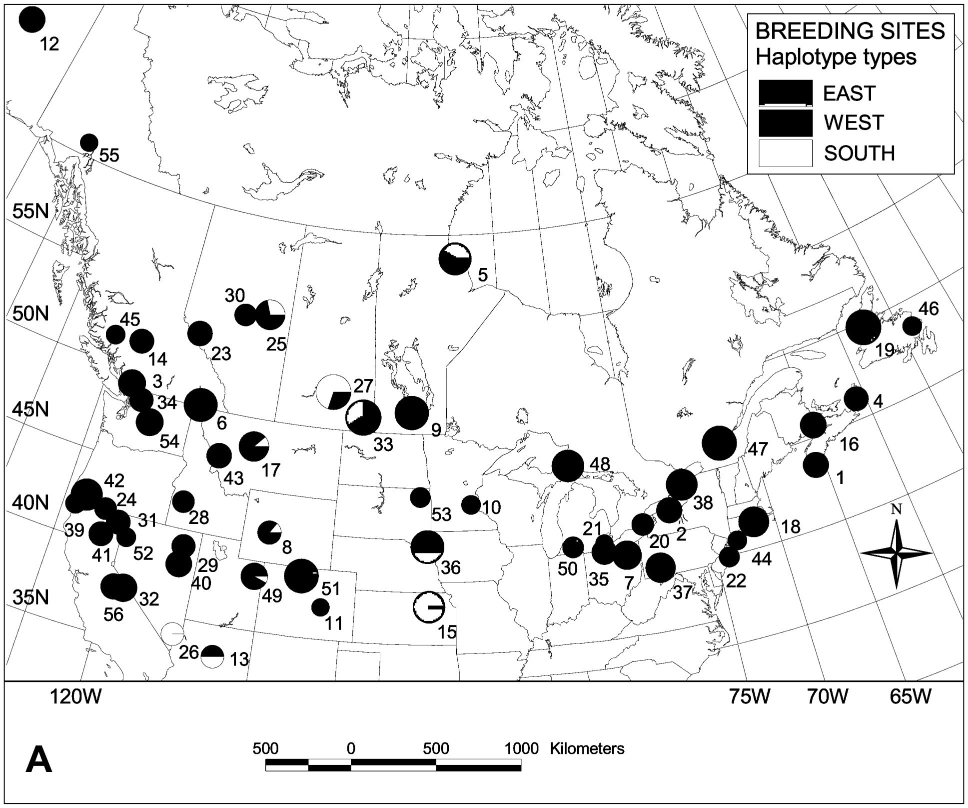


FIG. 1. Distribution of eastern, southern, and western haplotypes (A) found in northern yellow warblers captured on the breeding grounds ($n = 684$) and corresponding predicted probabilities of observing eastern (B), southern (C), and western (D) haplotypes. The size of each pie-chart is proportional to the number of samples for a specific site. The number below each pie-chart corresponds to an identification number for each site (see Appendix 2 for site names and coordinates). (*Continued on next page.*)

interaction between latitude and longitude of the sampling sites (multicategory logit model, longitude: Wald $\chi^2 = 63.35$, df = 2, $P < 0.001$; latitude: Wald $\chi^2 = 45.29$, df = 2, $P < 0.001$; longitude*latitude: Wald $\chi^2 = 49.40$, df = 2, $P < 0.001$, $r^2 = 1.00$; Fig. 1), which means the overall distributions of the lineages were generally but not always parallel to each other. In fact, the longitude*latitude interaction was essentially caused by the localized distribution of southern haplotypes in the southwest United States, because only longitude explained the spatial distribution of eastern and western lineages after removal of the southern lineage from the analysis (logistic model with longitude: Wald $\chi^2 = 66.30$, df = 1, $P < 0.001$; map not shown).

The geostatistical analysis defined three zone types: (1) an exclusion zone, where a lineage was nearly absent (10% genetic contour); (2) an abundance zone, where a lineage was extremely abundant (90% genetic contour); and (3) an overlap zone, where a specific lineage shared the breeding area with another lineage (area between 10% and 90% genetic contours). For the eastern lineage, the exclusion zone was located at 109°W longitude in the United States but diverted westward to 116°W longitude in northern Canada, whereas the abundance zone was located east of 95°W longitude in the United States but diverted eastward to 85°W longitude in Ontario (Fig. 1). In the western lineage, the exclusion zone matched the eastern abundance zone. The western abundance zone broadly followed 110°W longitude contour but diverted westward when it reached 40°W latitude in the Rocky Mountains in the United States (Fig. 1). By contrast, the exclusion zone of the southern lineage encompassed most of North America,

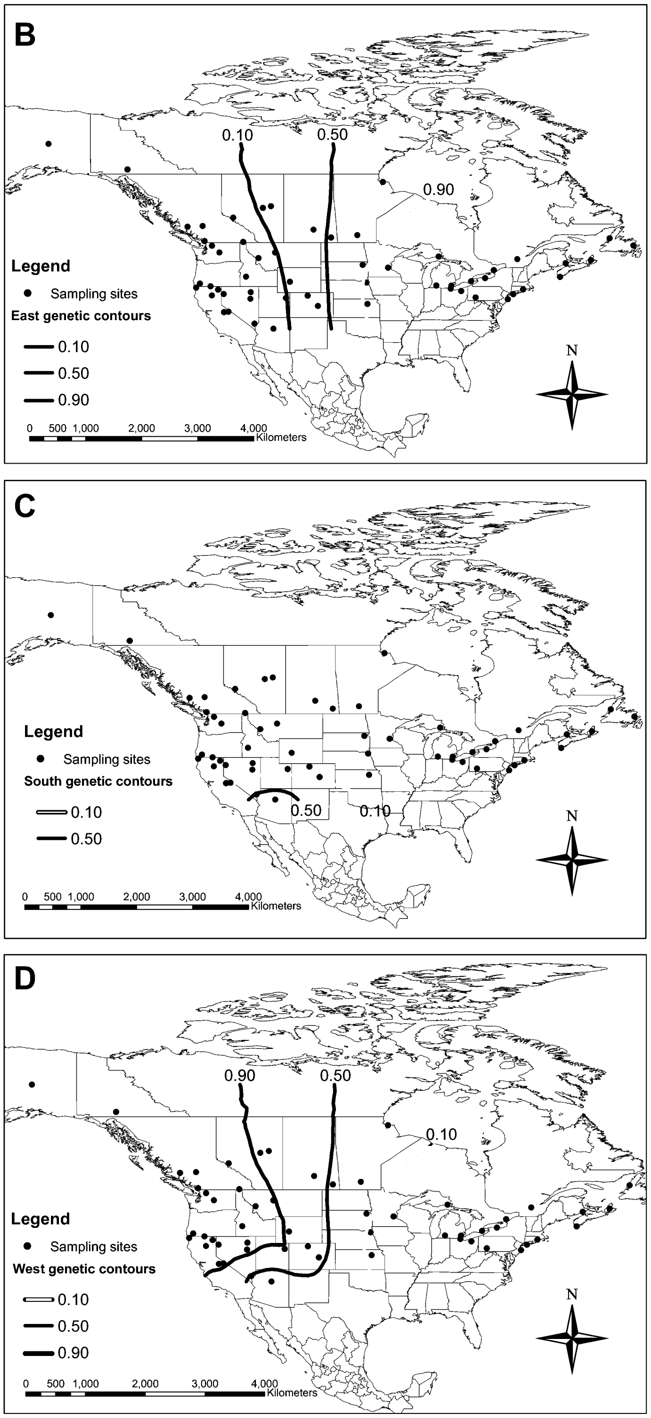


Fig. 1. (*Continued.*) Predicted probabilities of observing eastern (B), southern (C), and western (D) haplotypes on the breeding grounds.

whereas the abundance zone (with a 75% genetic contour in this case) was restricted to New Mexico (Fig. 1). The east–west overlap zone was particularly extensive and ranged from 1,300 km in the United States to >3,000 km in northern Canada (Fig. 1). The west–south overlap zone was sharp, and was only 500 km wide (Fig. 1).

Connectivity Using Mitochondrial DNA as a Longitudinal Marker

Wintering grounds.—On the wintering grounds, eastern haplotypes were mainly found in Venezuela but were also present in the Yucatan Peninsula (Mexico) and in Panama, whereas western haplotypes were very common along the Pacific coast of Mexico but were also found in the Yucatan Peninsula, Belize, and Panama (Fig. 2). The southern haplotypes were limited to southwestern Mexico—Jalisco ($n = 1$), central Michoacan ($n = 3$), and central Oaxaca ($n = 1$)—thus showing possible links with breeding populations in the southwestern United States. This low occurrence on the wintering grounds may be linked to insufficient sampling in northern Mexico and to the smaller population size of this lineage, as suggested by the localized breeding distribution (see Fig. 2). Not surprisingly, the proportion of eastern haplotypes increased with increasing longitude on the wintering grounds (logistic model where x = longitude, $\pi_{\text{east}} = \exp(26.11 + 0.31x) / 1 + \exp(26.11 + 0.31x)$, Wald $\chi^2 = 28.68$, df = 1, $P < 0.0001$, $r^2 = 0.57$). Using a geostatistical model, we determined that the abundance zone of the eastern lineage was in South America (Venezuela), whereas the abundance zone of the western lineage was west of the Yucatan Peninsula in Mexico (Fig. 2). Thus, there was strong connectivity between (1) Venezuela and the eastern abundance zone found on the breeding grounds (east of longitude 95°W in the United States and east of longitude 85°W in Ontario); (2) western Mexico and the western abundance zone found on the breeding grounds (west of longitude 115°W in northern Canada and west of longitude 110°W in the United States). The overlap zone was at least 1,750 km wide (i.e., about the average distance of the overlap zone found on the breeding grounds). In summary, the mtDNA lineages were strongly structured on the wintering sites, but this strong structure was partly driven by the absence of western birds in Venezuela.

Migration stopovers.—During spring migration, eastern haplotypes were also present in eastern and central North America, whereas western haplotypes were present in western and central North America (Fig. 3). Southern haplotypes were observed only in the southwestern United States during spring migration (Beatty, Nevada: $n = 2$; Alamo, Nevada: $n = 1$; Buenos Aires, NWR AZ: $n = 1$). The proportion of eastern haplotypes was highest at easternmost longitudes (logistic model where x = longitude, $\pi_{\text{east}} = \exp(39.66 + 0.41x) / 1 + \exp(39.66 + 0.41x)$, Wald $\chi^2 = 20.43$, df = 1, $P < 0.0001$, $r^2 = 0.66$; Fig. 3). In general, the individuals of the eastern lineage did not migrate west of longitude 105°W, whereas individuals of the western lineage did not migrate east of longitude 92°W. Thus, stopovers located in the eastern spring migration zone were tightly linked with breeding sites in eastern North America and with wintering sites in Venezuela, whereas stopovers located within the western migration zone were tightly linked with breeding sites in western North America and with wintering sites in Mexico. The overlap zone was centered on longitude 97°W (i.e., the 50% genetic contour), spanned Manitoba and the U.S. Central Great Plains, and was ~1,250 km wide.

The distribution of eastern and western lineages during fall migration showed the same general pattern as on the breeding grounds and spring stopovers (eastern haplotypes in eastern and central North America, western haplotypes in western and central North America; Fig. 4), but no southern haplotypes were found. In fall migration, the proportion of eastern haplotypes significantly increased with increasing longitude and decreasing latitude (logistic model where x = longitude and y = latitude, $\pi_{\text{east}} = \exp(31.59 + 0.28x - 0.15y) / 1 + \exp(31.59 + 0.28x - 0.15y)$, longitude: Wald $\chi^2 = 89.57$, df = 1, $P < 0.0001$; latitude: Wald $\chi^2 = 13.43$, df = 1, $P = 0.0002$, $r^2 = 0.61$; Fig. 4). This latitudinal pattern was not found in the spring and was possibly a sampling artifact because of the absence of samples from Texas. Also, western birds tended to migrate farther into the eastern part of the continent than in spring, because the 50% genetic contour was shifted beyond longitude 97°W. The overlap zone was ~1,625 km wide.

Annual migration patterns.—Depending on their lineage, northern yellow warbler individuals were present at distinct locales during the

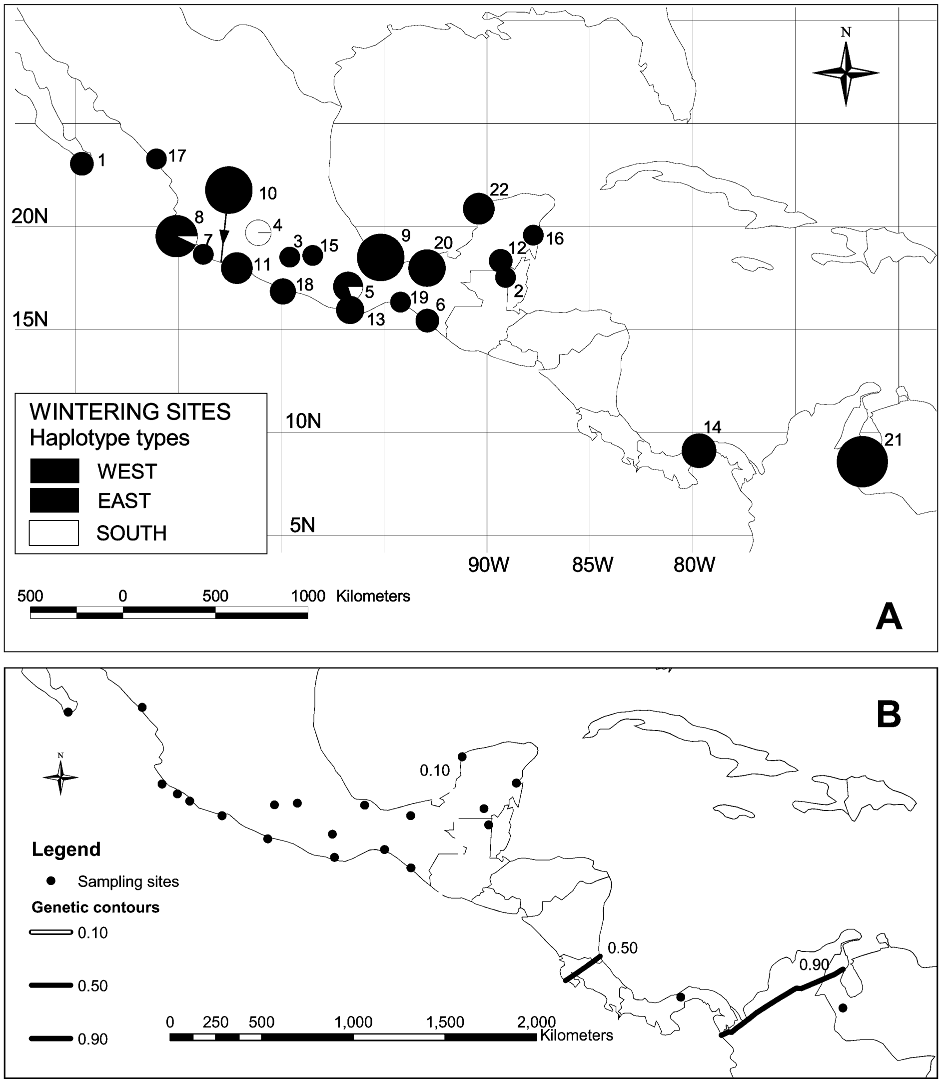


FIG. 2. Distribution of eastern, southern, and western haplotypes (A) found in northern yellow warblers captured on the wintering grounds ($n = 133$) and predicted probabilities of observing eastern haplotypes on the wintering grounds (B). The size of each pie-chart is proportional to the number of samples for a specific site. The number below each pie-chart corresponds to an identification number for each site (see Appendix 2 for site names and coordinates).

annual cycle: the season and the mtDNA lineage of an individual strongly determined where in terms of geographic location this individual would be (season: $F = 283.07$, df = 6 and 3,172, $P < 0.0001$; haplotype: $F = 762.34$, df = 2 and 1,585, $P < 0.0001$; Fig. 5) and explained 70% and 49% of the variance in the geographic position of birds, respectively (Table 1). The season*haplotype interaction was significant ($F = 21.53$, df = 6 and 3,172, $P < 0.0001$) but explained only 8% of the variance. This interaction suggests that the migratory routes of eastern and western birds were not always perfectly parallel to each other during the annual cycle and had little ecological meaning (Fig. 5). We further examined the effects of season and haplotype types on the longitudinal and latitudinal distributions alone using univariate models. These variables and

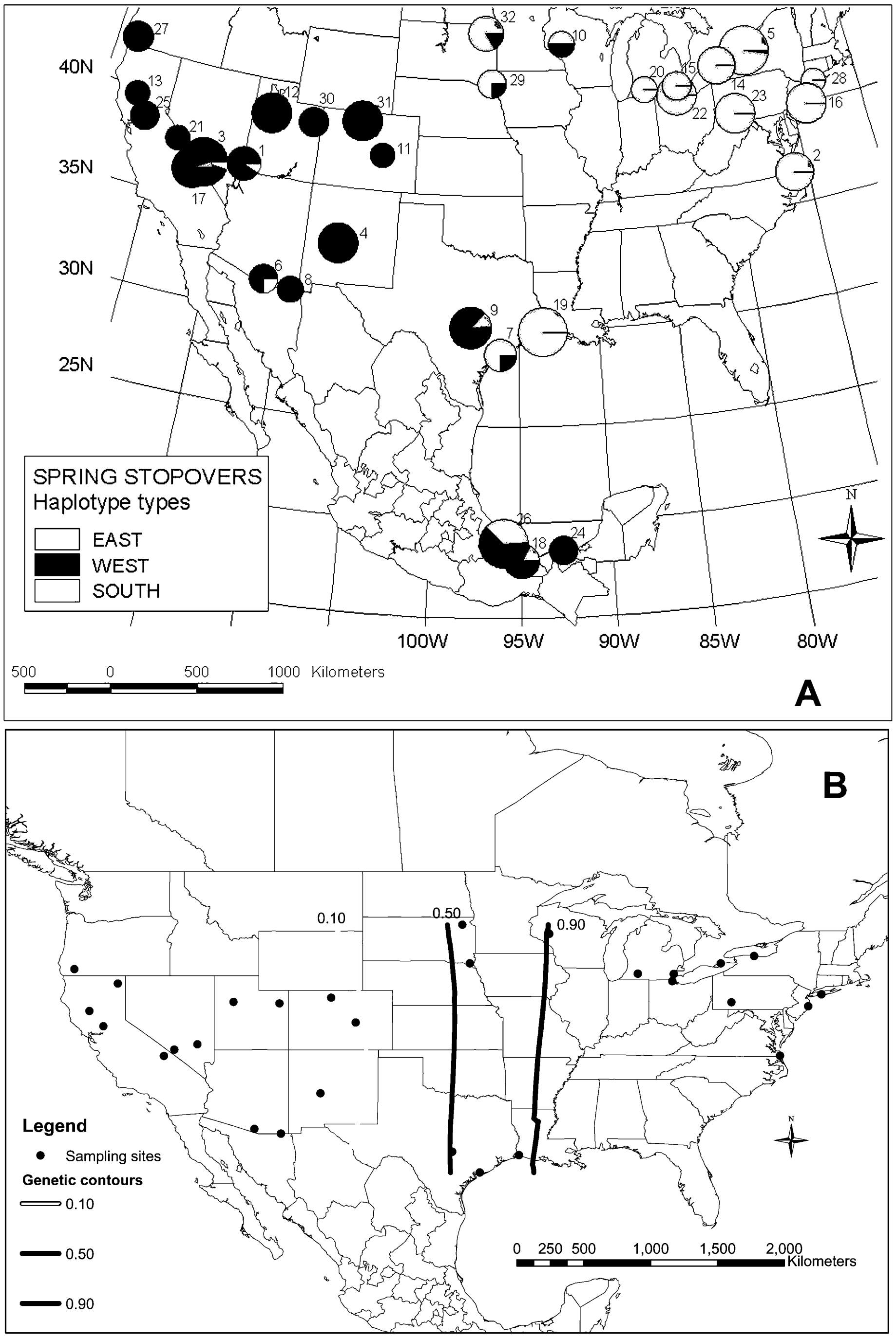


Fig. 3. Distribution of eastern, southern, and western haplotypes (A) found in northern yellow warblers captured on spring stopovers ($n = 438$) and predicted probabilities of observing eastern haplotypes on spring stopovers (B). The size of each pie-chart is proportionate to the number of samples for a specific site. The number below each pie-chart corresponds to an identification number for each site (see Appendix 2 for site names and coordinates).

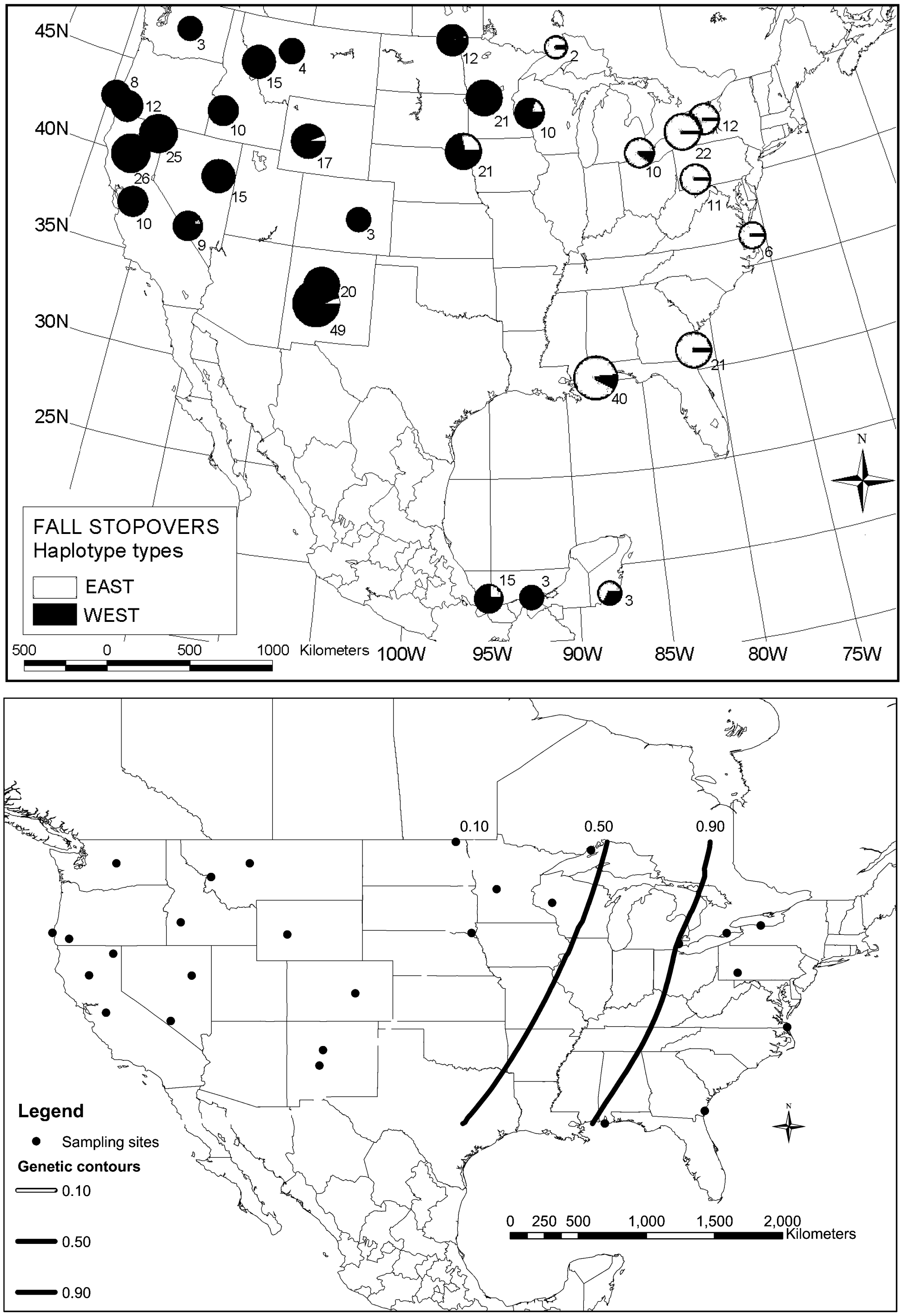


FIG. 4. Distribution of eastern and western haplotypes (A) found in northern yellow warblers captured on fall stopovers ($n = 428$) and predicted probabilities of observing eastern haplotypes on fall stopovers (B). No individual of the southern lineage was obtained for this season. The size of each pie-chart is proportional to the number of samples for a specific site. The number below each pie-chart corresponds to an identification number for each site (see Appendix 2 for site names and coordinates).

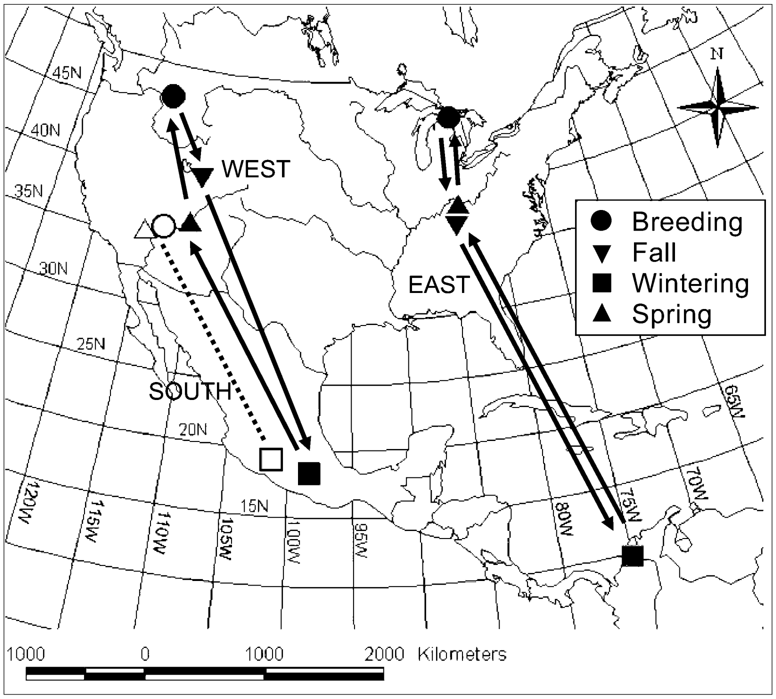


FIG. 5. Summary of migration patterns in northern yellow warbler lineages. Symbols refer to the average geographic position of a lineage for a given season based on least-square means of a MANOVA. Arrows indicate lineage movements between seasons. Note that only the eastern (gray) and western (black) lineages were used in the model. Southern lineage (white) was excluded from analysis because sample size was too small. However, the average geographic position of sites where this lineage was observed is plotted on the graph.

their interaction significantly explained the longitudinal distribution (F = 409.7, df = 7 and 1,586, $P < 0.0001$, $r^2 = 0.64$) and the latitudinal distribution (F = 569.2, df = 7 and 1,586, $P <$ 0.0001, $r^2 = 0.72$) of birds (Table 1). Although haplotype type was the best predictor explaining longitudinal location, season best predicted latitudinal location of birds (Table 1).

On the breeding grounds, eastern and western birds settled in habitats located at very distinct longitudes (test of simple effects, F = 1499.00, df = 1, $P < 0.0001$; Fig. 5 and Table 1). During fall migration over Canada and the United States, western birds headed southeast because they encountered the Pacific Ocean, whereas eastern birds took a more southerly direction over the eastern United States. Although their routes converged during migration, eastern and western birds used, on average, stopovers located at different longitudes (F = 545.56, df = 1, $P < 0.0001$). On their way to the wintering grounds, eastern and western birds tended to migrate in the same general direction (south-southeast) but encountered different obstacles: eastern birds flew across the Gulf of Mexico and the Caribbean, whereas western birds crossed the arid lands of the southwestern United States. Eastern and western birds segregated longitudinally and latitudinally on the wintering grounds, with eastern birds settling in wintering habitats located southeast (i.e., mostly in South America) of the habitats occupied by the western birds, mostly in Mexico (longitude: F = 112.99, df = 1, $P < 0.0001$; latitude: F = 66.66, df = 1, $P < 0.0001$). In spring, eastern and western birds headed back to stopovers located in the United States, taking the same general direction (north-northwest) over the same broad regions and geographic barriers as in spring. They remained segregated on stopovers (longitude: F = 608.74, df = 1, $P < 0.0001$). Once over the United States, western birds kept the same direction (north-northeast), whereas eastern birds headed north to their breeding grounds.

Table 1. Summary statistics of multivariate and univariate models explaining the distribution of eastern and western lineages throughout the annual cycle.

(A) MANOVA: Longitude and latitude

Source	Pillai's trace statistic	df	*F*	*P*
Season	0.70	6 and 3,172	283.1	<0.0001
Haplotype	0.49	2 and 1,585	762.3	<0.0001
Season*haplotype	0.08	6 and 3,172	21.5	<0.0001

(B) Least-square means obtained from MANOVA and 95% confidence intervals

Season	Haplotype	Longitude (°W)	95% CI Longitude (°W)	Latitude (°N)	95% CI Latitude (°N)
Breeding	East	83.37	84.47 to 82.26	45.70	45.17 to 46.23
Breeding	West	115.16	116.33 to 113.99	46.55	45.99 to 47.11
Fall	East	84.31	86.12 to 82.50	36.94	36.08 to 37.80
Fall	West	110.47	111.71 to 109.22	40.56	39.97 to 41.16
Winter	East	83.70	85.17 to 82.24	38.66	37.96 to 39.36
Winter	West	110.74	112.32 to 109.17	36.90	36.15 to 37.65
Spring	East	74.97	78.72 to 71.22	9.70	7.90 to 11.48
Spring	West	98.33	100.46 to 96.20	18.25	17.23 to 19.26

(C) ANOVA: Longitude only ($F = 409.7$, df = 7 and 1,586, $P < 0.0001$, $r^2 = 0.64$)

Source	df	Type III sum of squares	Mean square	*F*	*P*
Season	3	13,173.9	4,385.6	38.9	<0.0001
Haplotype	1	166,972.7	166,972.7	1,474.8	<0.0001
Season*haplotype	3	3,116.3	1,028.1	9.2	<0.0001

(D) ANOVA: Latitude only ($F = 569.2$, df = 7 and 1,586, $P < 0.0001$, $r^2 = 0.72$)

Source	df	Type III sum of squares	Mean square	*F*	*P*
Season	3	91,014.0	30,338.0	1,179.5	<0.0001
Haplotype	1	1,805.6	1,805.6	70.2	<0.0001
Season*haplotype	3	2,636.7	878.9	34.2	<0.0001

Connectivity Using a Latitudinal Marker: Stable Hydrogen Isotope Ratios

Forty-six percent (549.78 of 1206.06) of the variation in δD values was associated with haplotype type, whereas the remaining variation was attributable to other factors. Range of δD values was widest in the western lineage (–185.30‰ to –38.80‰), intermediate in the eastern lineage (–140.50‰ to –44.90‰), and smallest in the southern lineage (–93.60‰ to –54.11‰) (but see Table 2). Stable hydrogen isotope values differed among birds from different mtDNA lineages: western birds had a δD mean value (–127.15‰) that was significantly more negative than the δD mean values of eastern (–94.00‰) and southern (–82.09‰) birds (permutation tests in PERM; $P \leq 0.001$ for both tests), which suggests, on average, a more northern breeding origin. Overall, these results are concordant with the geographic distribution of the mtDNA haplotypes: western haplotypes were present along the Pacific coast, along the Rocky Mountains, and in central North America, where the δD ratios corrected for feathers tend to be lower (often less than –95‰); eastern haplotypes were present in eastern and central North America, where the δD values are intermediate (–115‰ to –50‰); and southern haplotypes were restricted to the southwestern United States, where the δD values are highest (–95‰ to –50‰) (Wassenaar and Hobson 2000). Furthermore, the breeding distribution of the northern yellow warbler reaches more northerly latitudes in the western part of the continent (~70°N latitude) than in the eastern part of the continent (just beyond 55°N latitude; Dunn and Garrett 1997).

Thirty-four percent (218.587 of 640.395) of the variance in δD values can be explained by differences among wintering sites. Thus, some wintering areas differed in their stable hydrogen isotope ratios (Table 3). In particular,

TABLE 2. Feather δD values of northern yellow warbler lineages. Data were collected on all sites and seasons (*n* = number of individuals sampled for each lineage).

Lineage	*n*	Mean ± SD (‰)	25th and 75th quartiles	Range (‰)
Eastern	149	–94.00 ± 19.97	–107.20 to –78.05	–140.20 to –44.90
Western	253	–127.15 ± 28.57	–145.35 to –113.94	–185.30 to –38.80
Southern	6	–82.05 ± 14.94	–93.23 to –72.18	–82.08 to –54.11

TABLE 3. Summary of δD values of flight feathers from northern yellow warblers (*n* = 94) collected in eight wintering sites (*n* = number of individuals sampled). n/a = option not available.

Sites	*n*	Haplotype types	Mean ± SD (‰)	Range (‰)
Mexico				
Guerrero	8	8 west	–110.9 ± 8.3	–95.9 to –121.7
Jalisco	9	1 south	n/a	–54.1
		8 west	–125.6 ± 19.9	–108.1 to –169.5
Michoacan	22	3 south	–85.1 ± 7.8	–78.2 to –93.
		19 west	–124.4 ± 18.7	–89.3 to –158.7
Tabasco	10	10 west	–150.5 ± 15.4	–125.9 to –167.9
Veracruz	18	18 west	–135.5 ± 20.6	–100.5 to –171.3
Yucatan	5	1 east	n/a	–79.1
		4 west	–148.8 ± 14.0	–138.0 to –163.9
Panama				
Canal zone	7	3 east	–109.2 ± 8.1	–101.0 to –117.2
		3 west	–120.6 ± 16.4	–116.7 to –138.6
		1 unknown[a]	n/a	–106.7
Venezuela				
Zulia and Merida states	15	15 east	–102.6 ± 15.0	–77.7 to –133.2

[a] DNA could not be amplified.

TABLE 4. Values of *P* of pairwise comparisons between δD mean values of eight wintering areas. Values were obtained by permutations (1,000 resampling events for each of 10 iterations). Significant comparisons after sequential Bonferroni corrections are indicated by an asterisk.

	Jalisco	Michoacan	Panama	Tabasco	Venezuela	Veracruz	Yucatan
Guerrero	0.551	0.255	0.645	0.000*	0.106	0.004	0.078
Jalisco	–	0.786	0.745	0.005	0.085	0.081	0.347
Michoacan		–	0.460	0.001*	0.007	0.029	0.242
Panama			–	0.001*	0.065	0.017	0.156
Tabasco				–	0.000*	0.058	0.227
Venezuela					–	0.000*	0.005
Veracruz						–	0.948

Tabasco had a more negative δD mean value than Guerrero and Michoacan on the western side and Panama and Venezuela on the eastern side (permutation tests in PERM, $P \leq 0.001$; Table 4). Tabasco and Veracruz had the most negative δD ratios (mean: –135.5‰ and –150.5‰, respectively) and were primarily composed of birds coming from northern latitudes and boreal and taiga ecosystems. The Venezuelan site had the highest δD value (mean = –102.6‰; Table 3) and, thus, was primarily composed of birds coming from southerly latitudes and temperate habitats.

Latitude of wintering sites explained 30% of the total variance (192.132 of 444.012). There was a marginal relationship between the latitude of sampling sites and feather δD values (F = 3.99, df = 1 and 6, P = 0.09, r^2 = 0.632; Fig. 6), possibly driven by higher isotope values found in the eastern haplotypes that were mainly present in the southernmost wintering site (i.e., Venezuela at latitude 8.50°N; Fig. 6). In fact, δD

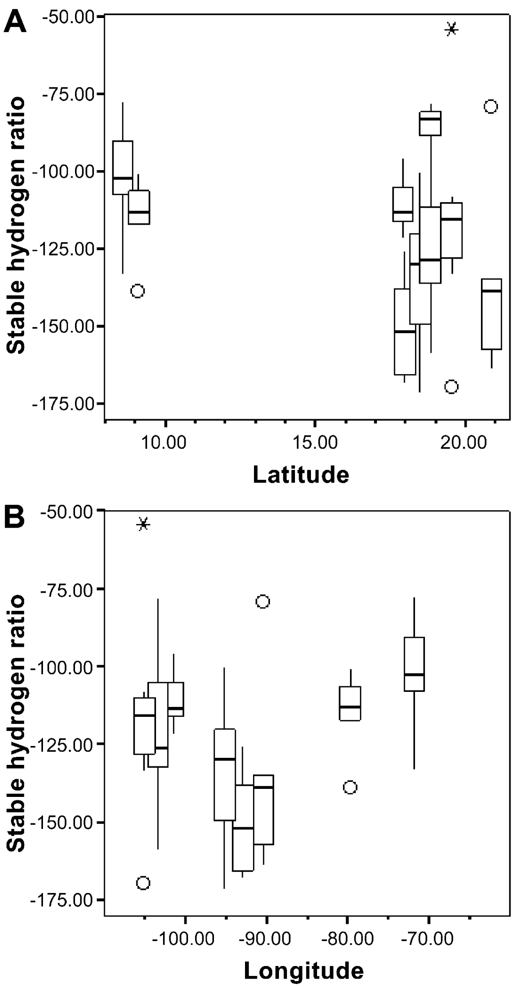


FIG. 6. Stable hydrogen isotope values (‰) measured in flight feathers of wintering northern yellow warblers plotted against (A) latitude and (B) longitude of the wintering sites (n = 8 sites).

values did not vary with the latitude of wintering sites within the western lineage (F = 0.241, df = 1 and 6, P = 0.64, r^2 = 0.05). We did not test this relationship within the eastern lineage because of the limited number of sites with eastern haplotypes.

Longitude of wintering sites explained a larger proportion of the total variance than latitude (41% or 262.553 or 642.553). Stable isotope analysis also revealed weak longitudinal connectivity. Specifically, the longitude of sampling sites had significant linear and quadratic effects on δD values (F = 9.27, df = 2 and 5, P = 0.02, r^2 = 0.79; linear effect only: F = 15.80, df = 1, P = 0.01; quadratic effect only: F = 15.09, df = 1, P = 0.01; Fig. 6), which means that birds at westerly and easterly longitudes were, on average, from more southerly (temperate) areas than birds from more central longitudes, which were in turn from more northerly (boreal) areas. This pattern mirrors the variation in the abundance of breeding northern yellow warblers in North America and the shape of stable hydrogen contours present on the breeding grounds, where the most negative ratios are found in north-central Canada (Appendix 3). Within the western lineage only, the δD values did not vary with the longitude of sites (linear and quadratic model, F = 2.88, df = 2 and 4, P = 0.17, r^2 = 0.59).

MIGRATION FLYWAYS

We compared feather δD values between sites to identify stopovers with relatively similar mean δD values (e.g., sites that receive the same pool of birds; Table 5). In spring, stopovers had significantly distinct isotopic signatures that clustered into three groups: Bosque del Apache (permutation tests, mean = –63.6‰) differed from all other sites, Beatty and Salinas (permutation tests, means = –116.7‰ and –121.9 ‰, respectively) differed from all other sites together, whereas Sabine NWR and Braddock Bay (permutation tests, means = –77.7‰ and –83.8‰, respectively) differed from all other sites as well (Table 6 and Fig. 7). These results suggest the presence of three possible flyways during that season. In fall, the stopovers also had significantly different isotopic signatures but clustered into only two groups: Fort Morgan received migrants with higher δD values (permutation tests, mean = –110.6‰) than Glenn and Tehama counties and Bosque del Apache, whereas Glenn and Tehama counties and Bosque del Apache did not differ from each other (permutation tests, means = –126.9‰ and 133.7‰, respectively) (Table 6 and Fig. 7). Thus, Fort Morgan was possibly located along a different flyway than Bosque del Apache and Glenn and Tehama counties together.

Bosque del Apache was the only site surveyed for both spring and fall migration within the same year. There, δD values of fall migrants were significantly more negative than those of spring migrants, which means that birds breeding in northern areas were more common in fall than in spring during the sampling period

Table 5. Summary of δD values of flight feathers from northern yellow warblers (*n* = 347) captured on spring and fall stopovers (*n* = number of individuals sampled). "Eastern," "southern," and "western" refer to the haplotype lineage of samples that were genotyped, whereas unknown refers to samples that were not genotyped (n/a = option not available).

Stopovers	*n*	Mean ± SD (‰)	Range (‰)
	Spring migration		
Beatty, Nevada	South: 2	–91.6	–90.0 & –93.0
	West: 36	–120.5 ± 25.5	–58.2 to –171.3
	Unknown: 11	–108.2 ± 23.1	–73.4 to –152.5
	Total: 49	–116.7 ± 25.1	–58.2 to –171.3
Bosque del Apache National Wildlife Refuge (NWR), New Mexico	West: 19	–64.4 ± 23.7	–38.8 to –134.6
	Unknown: 1	–47.5	n/a
	Total: 20	–63.6 ± 23.4	–47.5 to –134.6
Braddock Bay, New York	East: 40	–84.4 ± 11.3	–54.4 to –114.6
	West: 1	–76.3	n/a
	Unknown: 10	–82.4 ± 7.9	–70.0 to –95.6
	Total: 51	–83.8 ± 10.6	–54.4 to –114.6
Los Tuxtlas, Veracruz, Mexico	East: 1	–106.4	n/a
	West: 8	–151.1 ± 15.9	–126.7 to –172.1
	Total: 9	–146.1 ± 21.1	–106.4 to –172.1
Louisiana (Sabines National Wildlife Refuge)	Total (East): 31	–77.7 ± 11.5	–59.4 to –117.6
Salinas, Veracruz, Mexico	East: 15	–97.0 ± 20.1	–44.9 to –121.6
	West: 24	–129.7 ± 23.8	–50.4 to –185.3
	Unknown: 10	–140.4 ± 26.8	–87.5 to –165.1
	Total:49	–121.9 ± 28.6	–44.9 to –185.3
	Fall migration		
Fort Morgan, Alabama	East: 39	–109.2 ± 19.8	–80.2 to –140.5
	West: 3	–128.7 ± 21.5	–111.4 to –152.8
	Total: 42	–110.6 ± 20.3	–80.2 to –152.8
Glenn and Tehama counties, California	Total (West): 26	–126.9 ± 17.7	–94.4 to –155.7
Bosque del Apache NWR, New Mexico	East: 2	–128.0	–116.0 & –140.0
	West: 41	–134.0 ± 15.8	–104.0 to –180.0
	Total: 43	–133.7 ± 15.7	–104.0 to –180.0
Los Tuxtlas, Veracruz, Mexico	East: 2	–111.7	–106.4 & –119.0
	West: 4	–146.6 ± 10.3	–133.7 to –156.7
	Total: 6	–134.9 ± 20.2	–104.4 to 156.7
Westport, Minnesota	Total (West): 21	–155.4 ± 15.0	–110.4 to –177.3

TABLE 6. Values of P of pairwise comparisons between δD mean values of eight stopover sites. Values were obtained by permutations (1,000 resampling events for each of the 10 iterations). Significant comparisons after sequential Bonferroni corrections are indicated by an asterisk.

	Bosque[a]	Bosque[b]	Braddock[b]	Fort Morgan[a]	Glenn-Tehama[a]	Louisiana[b]	Salinas[b]
Beatty[b]	0.000*	0.000*	0.000*	0.205	0.071	0.000*	0.339
Bosque[a]	–	0.000*	0.000*	0.000*	0.102	0.000*	0.016
Bosque[b]		–	0.000*	0.000*	0.000*	0.005*	0.000*
Braddock[b]			–	0.000*	0.000*	0.017	0.000*
Fort Morgan[a]				–	0.001*	0.000*	0.037
Glenn and Tehama counties[a]					–	0.000*	0.417
Louisiana[b]						–	0.000

[a] Fall migration.
[b] Spring migration.

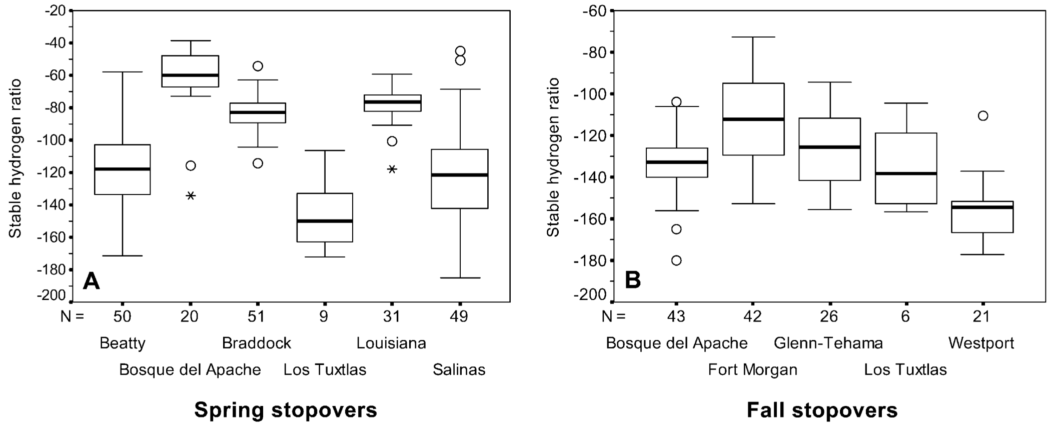


FIG. 7. Stable hydrogen isotope values (‰) plotted against (A) six spring stopover sites and (B) five fall stopover sites.

covered by the data (permutation test, $P < 0.001$; Table 6).

TWO-DIMENSIONAL CONNECTIVITY: GENETIC AND ISOTOPIC CONTOURS COMBINED

To pool information across both types of markers, we created assignment maps that partitioned the breeding range into four isotopic regions (A–D), overlaid by the 10% genetic contour of a specific lineage (Figs. 8–10). The 10% contour delimited an exclusion zone in which an individual of a specific haplotype was not likely to be found. We then assigned wintering individuals and migrants to subregions on the basis of their lineage and δD values. Venezuela exclusively had individuals from the subregions B-east and C-east (Fig. 11), which suggests that it was connected with breeding populations from various regions (i.e., U.S. Central Great Plains, Canadian Prairies, northeastern United States, and eastern Canada). In Panama, most birds originated from region C, or diverse geographic locales spanning from British Columbia down to Idaho then up to the Hudson Bay (Figs. 8–10). In Yucatan, the only eastern individual was from a large temperate subregion (B-east), whereas the four western individuals were from northern subregions (C-west and D-west). Tabasco and Veracruz had a large proportion of birds coming from north temperate to sub-Arctic regions (C-west and D-west; 100% and 95%, respectively), which suggests moderate links with more northern areas. Western birds from Guerrero had a more southerly breeding origin (B-west and C-west) that included diverse breeding regions: the U.S. Central Great Plains, the Canadian Prairies, the

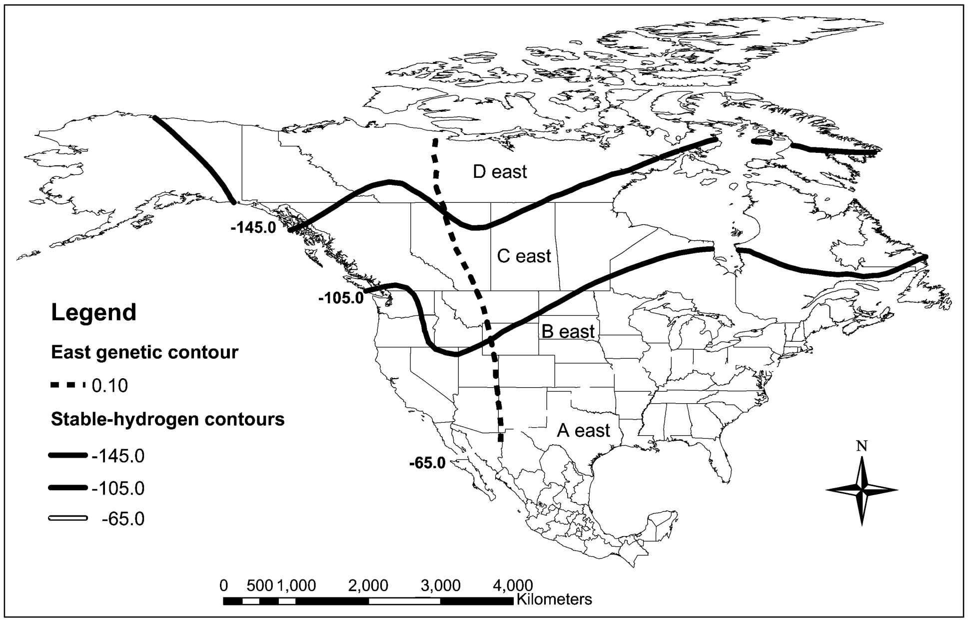


FIG. 8. Breeding subregions of eastern birds defined by δD values and genetic contours obtained by overlapping the kriging results of δD values for feathers with east predicted probabilities. The exclusion zone corresponds to the area west of the 10% east genetic contour (dashed black line).

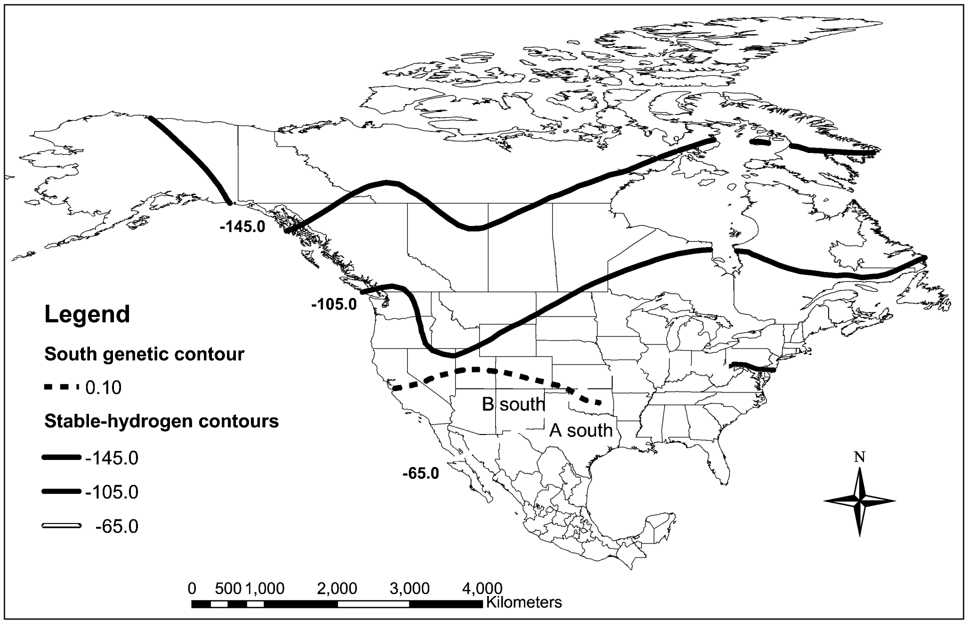


FIG. 9. Breeding subregions of southern birds defined by δD values and genetic contours obtained by overlapping the kriging results of δD values for feathers with south predicted probabilities. The exclusion zone corresponds to the area north of the 10% south genetic contour (dashed black line).

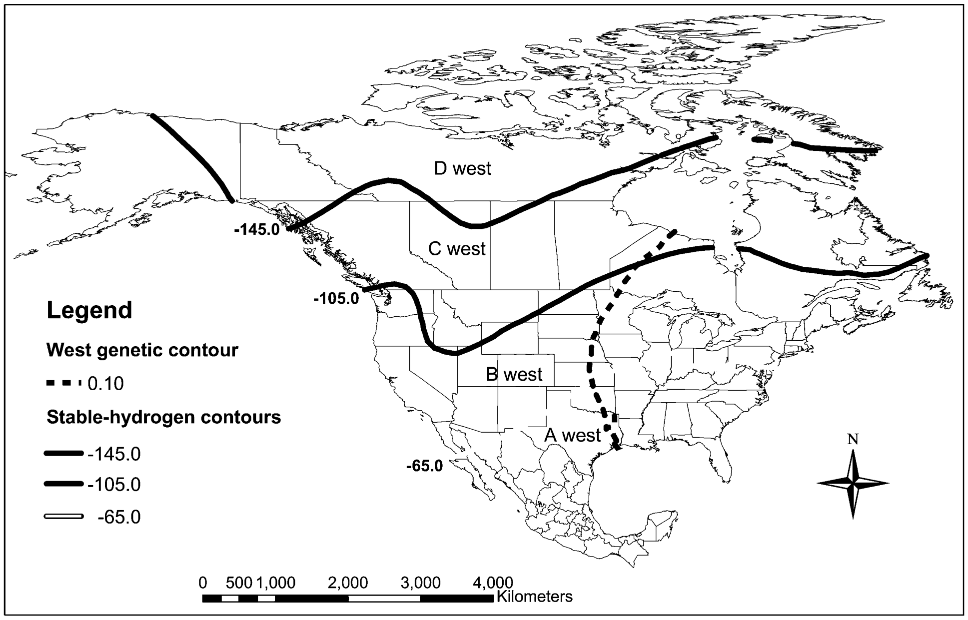


FIG. 10. Breeding subregions of western birds defined by stable hydrogen and genetic contours obtained by overlapping the kriging results of δD values for feathers with west predicted probabilities. The exclusion zone corresponds to the area east of the 10% west genetic contour (dashed black line).

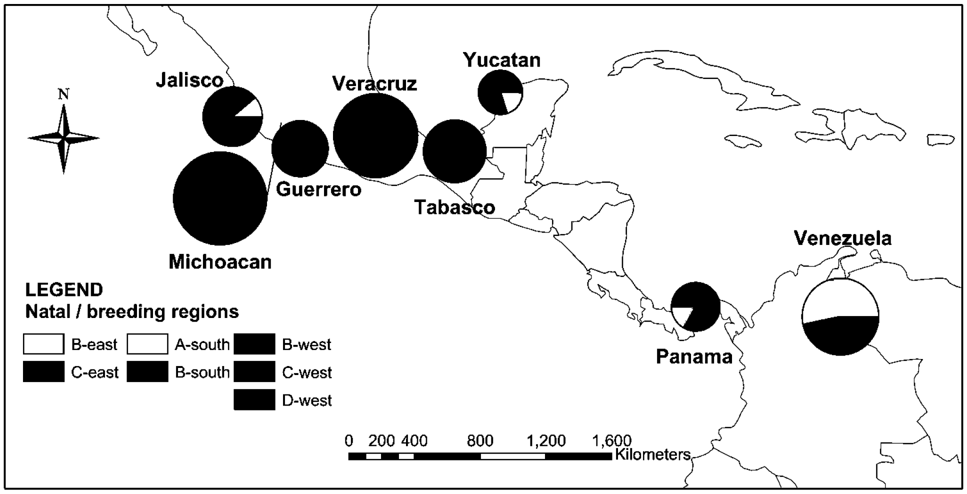


FIG. 11. Natal and breeding origins of 93 birds captured in eight wintering sites based on the δD values measured in their flight feathers and their haplotype lineage. We assigned birds using maps of breeding subregions. Pie-charts are proportional to the number of samples analyzed per site (see Table 3 for numbers).

Rocky Mountains, and the Pacific coast (Fig. 11). In Michoacan, birds from north temperate, boreal, and sub-Arctic areas (C-west, D-west; 77%) were next to birds from temperate regions (B-west, 9%) and even from arid areas of the southwestern United States (B-south, 14%). Jalisco included western birds from north-temperate to sub-Arctic regions (C-west and D-west, 89%) as well as a southern bird from the southwestern United States. In summary, birds from diverse ecosystems and geographic breeding locales (sometimes separated by as many as

4,000 km) often mixed on the same wintering site and showed no strong connectivity. There was possibly a weak pattern of connectivity in the western lineage, because birds of the northernmost subregion (D-west) were more common in eastern Mexico (Tabasco and Veracruz).

During spring migration in eastern North America, Louisiana and Braddock Bay, New York, had a very similar composition in natal and breeding origin of migrants: at least 80% of the migrants were from the subregion B-east (eastern Canada and northeastern United States west to the foot of the Rocky Mountains; Fig. 12). This result suggests that these two stopovers are along the same flyway (trans-Gulf route) and received birds mainly returning to temperate areas of eastern North America. In Beatty, Nevada, birds were almost exclusively from western subregions but had very diverse breeding origins, from local sites (southwest Colorado, southern Utah and Nevada, northern Arizona, and southern California) to northern sites (from the western shores of the Hudson Bay to the Pacific coasts of British Columbia). Thus, Beatty was not tightly linked with a particular area. Salinas, Veracruz, showed the greatest diversity in natal and breeding origins of migrants: birds came from three eastern subregions and three western subregions (Fig. 12A)—that is, from most parts of the breeding range, but especially intermediate (B-east) to high latitudes (C-west). The relatively high proportion of eastern migrants in this site (38%, 15 of 39) implies that Salinas was along a different flyway (circum-Gulf) than Beatty (western route), though these sites had similar isotopic signatures. In Bosque del Apache, New Mexico, most of the migrants analyzed were from the vicinity (mainly from subregion A-west; Fig. 12A). Bosque del Apache was thus probably located along a local end-point branch of a flyway based on this set of data. Los Tuxtlas, Mexico, which included museum specimens collected in the 1970s, comprised individuals from northerly latitudes (Fig. 12A).

During fall migration, Fort Morgan, Alabama, primarily received eastern migrants from temperate to boreal areas (B-east and C-east, 93%; Fig. 12B), confirming that it was located along the trans-Gulf route. By contrast, Westport, Minnesota, received migrants exclusively from boreal to sub-Arctic western subregions (D-west, 86%; Fig. 12B). The samples from this site consisted of a flock of migrants killed at a television tower during the night of 9–10 September 1962 (Raveling and Warner 1978). In the western part of the continent, Bosque del Apache, New Mexico, and Glenn and Tehama counties, California, had a relatively similar composition in natal and breeding origins of migrants (>70% from subregions C-west; Fig. 12B) and were probably along the same flyway (western route). Finally, Los Tuxtlas included migrants from a diverse array of locales (B-east, C-east, C-west, and D-west; Fig. 12B).

Connectivity Based on Banding Records

We identified six records of movements between breeding (individuals caught on breeding grounds during either the breeding or migration seasons in Canada or the United States; Fig. 13) and wintering locations. Most birds (5 of 6) were either banded or captured in Central America. Two birds were captured or recaptured in the eastern United States, one bird was from Alaska, and two birds were from the overlap east–west zone in the Canadian Prairies and the U.S. Central Great Plains. This diversity in breeding origins provides independent evidence that Central America receives migrants from a very wide array of breeding locales in North America and is an overlap zone where both lineages can be encountered. In terms of connectivity, this indicates that Central America is not tightly linked with a particular breeding area. The encounter of a bird breeding in Nevada in northwestern Mexico suggests possible connectivity between the southwestern United States and western Mexico, but additional encounters between these areas are required to confirm this pattern uncovered by the lineage distributions.

We obtained 46 records of movements over Canada and the United States (Fig. 14). The records occurred either between a migration season and the breeding season, between migration seasons, or within a migration season. Three patterns emerged. First, in eastern North America, large-scale movements were oriented east-northeast–west-southwest (Maritimes) or northeast–southwest (Ontario) and funneled over the eastern United States. Thus, there are strong links between breeding grounds in eastern Canada and stopovers in the eastern United States, which is concordant with the

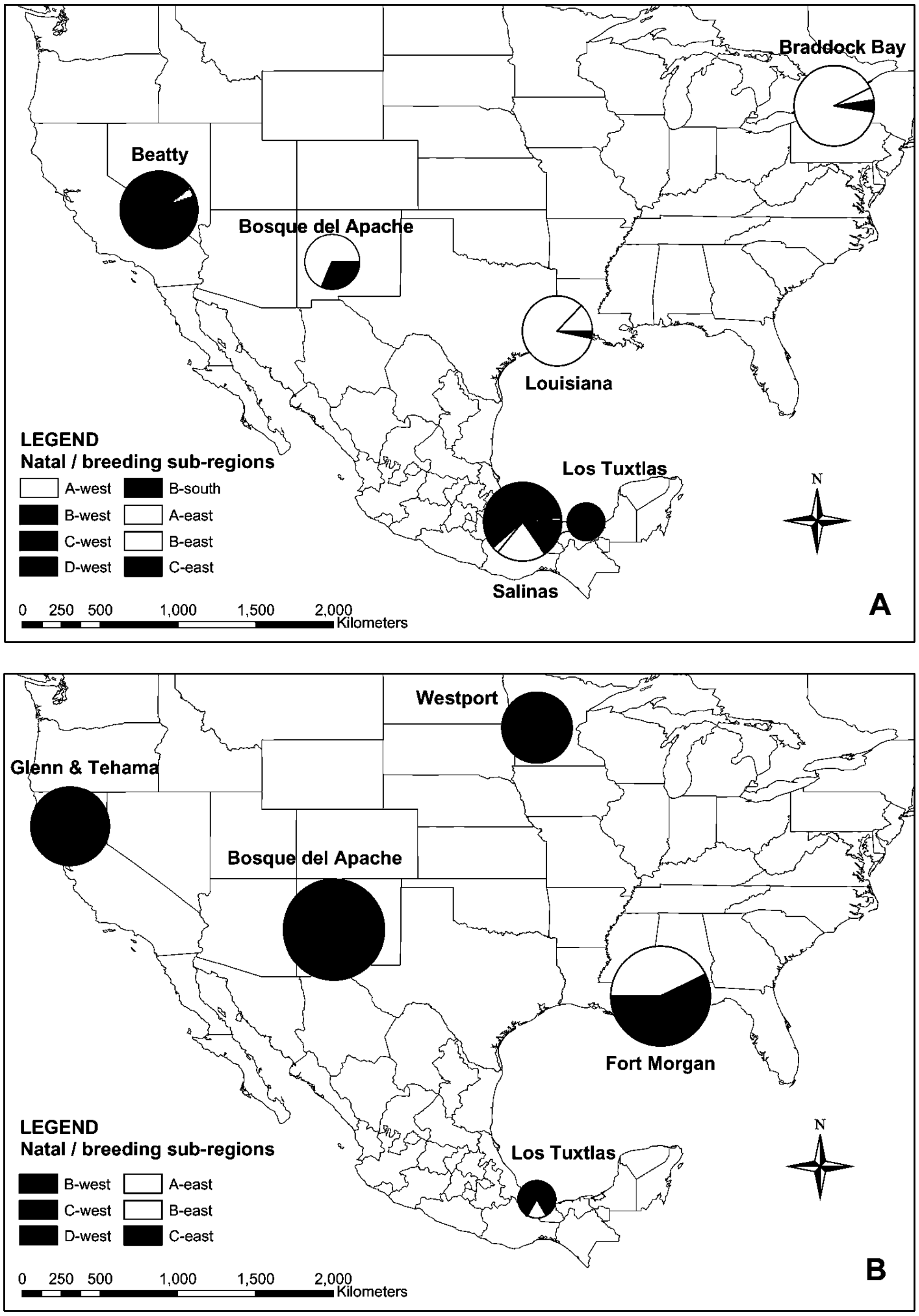


FIG. 12. Natal and breeding origins of 177 spring migrants (A) and 138 fall migrants (B) captured on stopover sites based on the δD values measured in their flight feathers and their haplotype lineage. We assigned birds using maps of breeding subregions. Pie-charts are proportional to the number of samples analyzed per site (see Table 5 for numbers).

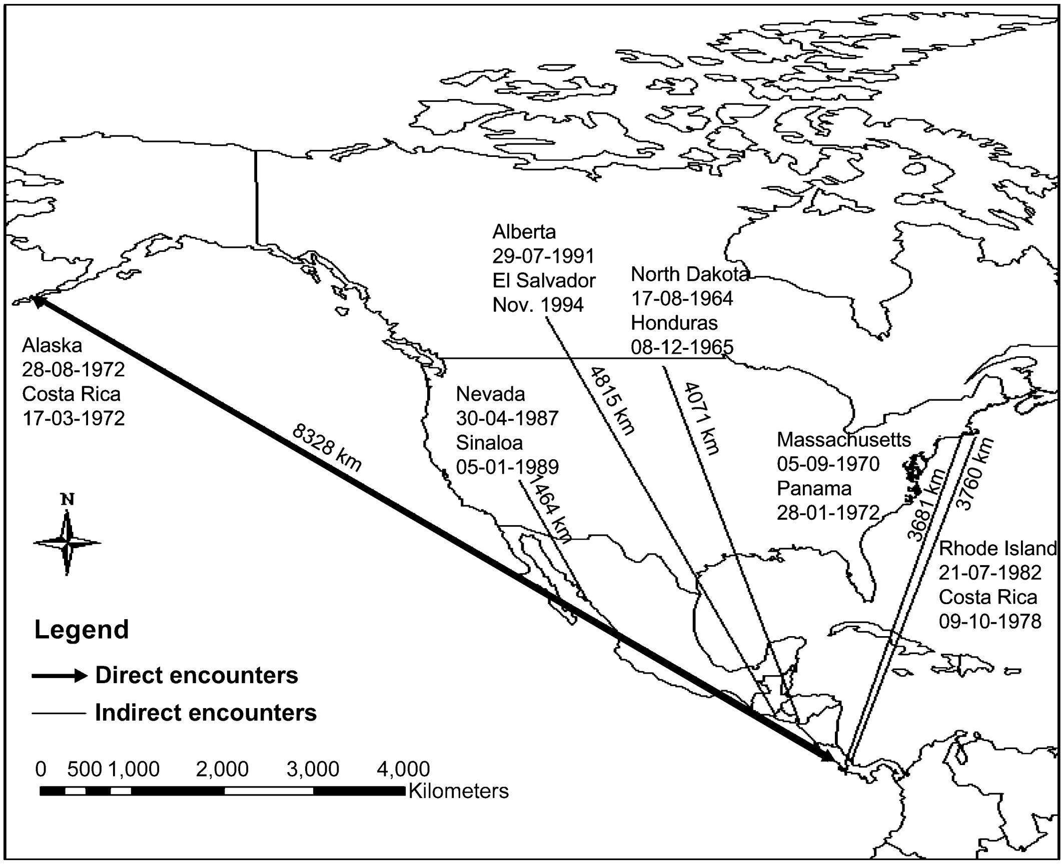


FIG. 13. Direct and indirect encounters showing possible movements of northern yellow warblers between Canada and the United States and the wintering range of this species. Data were obtained from the Migratory Bird Populations Division, National Wildlife Research Centre of the Canadian Wildlife Service, Ottawa.

lineage maps and overall migration patterns (Figs. 3–5). In western North America, movements tended to be along a northwest–southeast axis, and some birds possibly followed the coast of Alaska and British Columbia. Again, there is evidence of strong connectivity between breeding grounds and stopovers along the Pacific coast from Alaska to California. Finally, birds from central North America showed a greater diversity in migration axes (mainly the west-northwest–east-southeast, but also north-northwest–south-southeast and northwest–southeast) and breeding origins (from Minnesota to Alberta), which suggests no connectivity with a particular area. Some movements involving birds from the Canadian Prairies raise the possibility that birds of the western lineage are pushed toward easterly longitudes during migration, as suggested by the eastward shift of 50% genetic contours for spring and fall migration (Figs. 3 and 4) versus breeding season (Fig. 1).

In summary, the isotopic, genetic, and banding markers provided sufficient resolution to uncover a number of general patterns regarding migratory connectivity and flyways in the northern yellow warbler. (1) When we compared the distributions of the lineages throughout the annual range, we found evidence for strong longitudinal connectivity on a continental scale; (2) when we examined patterns of δD values among wintering sites, we found some evidence for weak regional connectivity; (3) eastern migrants used the trans-Gulf and circum-Gulf routes in spring and the trans-Gulf route in fall, whereas western migrants used the circum-Gulf and western routes in spring and fall; and (4) banding return data were relatively concordant with the genetic and isotopic data.

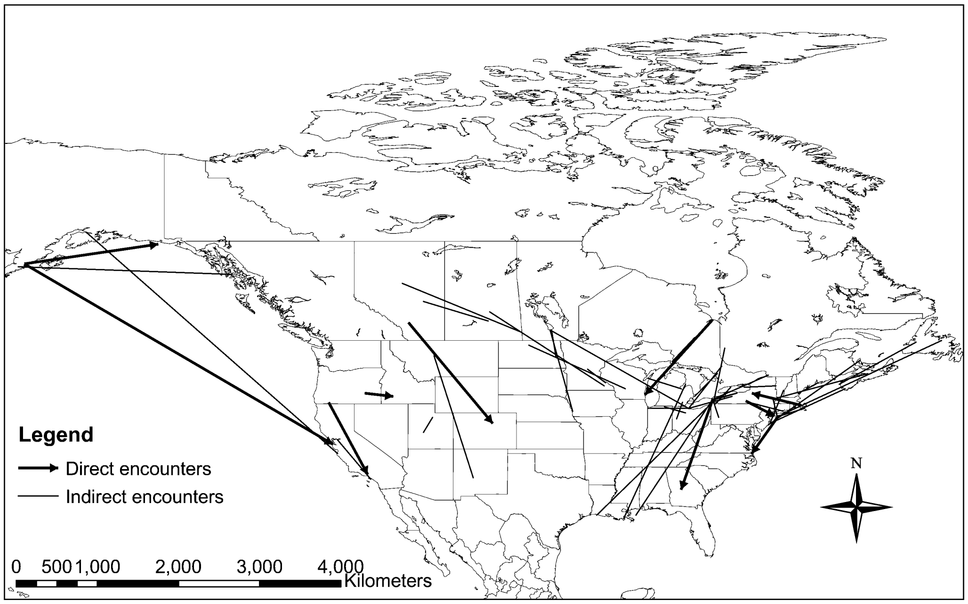


FIG. 14. Direct and indirect encounters showing possible movements of northern yellow warblers in Canada and the United States. The records occurred either between a migration season and the breeding season, between migration seasons, or within a migration season. Only birds with encounters ≥200 km from the banding sites are shown. Data were obtained from the Migratory Bird Populations Division, National Wildlife Research Centre at the Canadian Wildlife Service, Ottawa.

DISCUSSION

Our major finding was the presence of strong longitudinal connectivity at a continental scale (i.e., when the annual distributions of lineages were compared). Below, we discuss: (1) issues related to the resolution of markers in assessing migratory connectivity in a species with a very large geographic distribution; (2) historical factors that initially gave rise to the migration systems, and ecological factors that may promote and maintain them; and (3) evolutionary aspects and conservation implications of these migration systems.

RESOLUTION OF MARKERS: IS THERE UNDETECTED FINE-SCALE CONNECTIVITY?

Descriptions of migratory patterns are dictated by the degree of resolution of the markers used, and mtDNA is resolved only at a continental scale in the case of the eastern and western lineages. In terms of conservation applications, major questions that remain include the following: Is there any evidence of fine-scale connectivity? Is continental-scale connectivity the real pattern, or are we missing underlying population structure because of the mtDNA marker's lack of resolution? What other tools can we employ to verify this, and which ones should we use to detect fine-scale connectivity if it exists?

There is some evidence of fine-scale connectivity on the basis of the stable hydrogen data. Specifically, we found a weak quadratic relationship between longitude of wintering sites and feather isotopic ratios that was concordant with the isotopic contours on the breeding grounds. For example, stable isotope values in Tabasco tended to be more negative than those in sites located east or west of Tabasco. This finding suggests that from east to west, wintering habitats may receive birds from different longitudinal sections of the breeding grounds (i.e., birds would primarily be coming from diverse latitudinal breeding areas rather than diverse longitudinal breeding areas). According to this hypothesis, eastern wintering grounds would receive birds with high and less variable δD values, because breeding habitats in eastern North America do not reach extreme latitudes. Central wintering grounds would receive a higher proportion of birds with low δD values (i.e., more individuals coming from boreal and taiga breeding quarters where densities can be very high). Western wintering grounds would receive birds with slightly less-negative δD values. In the Wilson's Warbler, individuals from Baja California and western Mexico (which belonged to the western Wilson's Warbler lineage) had higher δD values than individuals from eastern Mexico, even though these sampling sites were located at the same latitude (Clegg et al. 2003). This pattern in Wilson's Warbler suggests weak connectivity between western North America and western Mexico and between north-central North America and eastern Mexico. In addition, American Redstarts wintering in Mexico (the westernmost part of the wintering range) tended to have lower stable hydrogen ratios than those wintering in the Greater and Lesser Antilles (the easternmost parts of the range) (Norris et al. 2006). Taken together, the results from these three Nearctic–Neotropical migrant species suggest the presence of parallel flyways. This hypothesis of parallel connectivity and flyways in North America should be tested in other long-distance migrants with broad breeding ranges, such as other wood warblers, vireos, thrushes, and flycatchers.

Could additional genetic markers be used to resolve fine-scale migratory connectivity? Here, we used categorical data (haplotype lineages) as opposed to using the full information content of mtDNA sequences. A hierarchical analysis of nucleotide diversity identified a major east–west split that accounted for 46% of the total genetic diversity of wintering populations (Boulet 2004). However, assignment of wintering populations to particular groups of breeding populations was not very successful. This likely reflects the limited differentiation of the mtDNA within lineages (Lovette et al. 2004, Boulet and Gibbs 2006). Microsatellite markers have been extensively used in phylogeographic studies, because they can screen the genetic variation at several biparentally inherited loci as opposed to a single, maternally inherited locus for mtDNA (Avise 2004). Using these multilocus markers, one can carry out population assignment tests to source migrants or wintering birds to breeding populations and determine a statistical support of the assignment (Webster et al. 2002, Piry et al. 2004). However, it is unlikely that microsatellite markers will detect fine-scale connectivity in migratory birds, because they show much less genetic differentiation across populations than mtDNA in several bird species, including the northern yellow warbler (Gibbs et al. 2000), Wilson's Warbler (Clegg et al. 2003), Grasshopper Sparrow (*Ammodramus savannarum*; Bulgin et al. 2003), and Common Eider (*Somateria mollissima*; Tiedemann et al. 2004). A better alternative may be to use amplified fragment length polymorphisms (AFLPs), which can generate numerous markers without intensive species-specific development. Because many loci can be surveyed simultaneously, this technique offers a great potential for identifying a small number of population-specific loci that can be used to assign individuals to particular populations with a high degree of certainty (Bensch et al. 2002a, b), even if the overall level of structure detected is not greater that than observed with mtDNA (Buehler 2003, Boulet et al. 2005).

Use of additional stable isotopes in combination with existing DNA information is another option for determining whether Nearctic–Neotropical migrants show migratory connectivity at a finer resolution than shown in the northern yellow warbler. By using a series of markers, one can dissect the bird's breeding range into regions that have a specific multivariate signature. Taking the northern yellow warbler as an example, one could first use the mtDNA marker to split the breeding range into three main regions (east, west, and south) and the stable hydrogen marker to obtain latitudinal resolution (and possibly weak longitudinal resolution), as in the present study. To better resolve the extended and partly overlapping eastern and western regions, one could further partition the breeding range using stable strontium ($\delta^{87}Sr$), which varies according to the geology of the soils (Hobson 2003). This isotope distinguished Black-throated Blue Warblers (*Dendroica caerulescens*) breeding in the Appalachian Mountains from those breeding in the Great Lakes basin (Chamberlain et al. 1997). In theory, stable strontium isotopes could distinguish, within the western lineage, northern yellow warblers breeding in the overlap zone in the Prairies from those breeding in northern areas and in the Rocky Mountains, because these three regions are located in different geological provinces (Geological Map of Canada, map

D1860A). Because this isotope offers a longitudinal resolution in central and western North America, it could be used to test the hypothesis of within-lineage parallel migration. However, no continental stable strontium isotope maps have been published to date (but see Beard and Johnson 2000); researchers would have to obtain stable strontium measurements in a number of ecosystems before assigning migrants and wintering birds to a breeding region.

Stable carbon isotope ($\delta^{13}C$) measurements, although primarily a latitudinal marker, has also the potential to resolve connectivity along an east–west axis in eastern North America: in Black-throated Blue Warbler, there was a significant longitudinal $\delta^{13}C$ pattern for birds in the northern part of the breeding range (Rubenstein et al. 2002). In addition, some carbon maps have been published (Hobson et al. 1999). The fact that in the northern yellow warbler, gene flow is more restricted away from the migration axis (east–west) than along the migration axis (north–south) suggests that northern yellow warbler populations are more structured along an east–west axis (Boulet and Gibbs 2006). It would be more productive to focus on markers that have the power to detect an east–west segregation. Other geochemical markers, such as trace elements and contaminants, may provide additional information at a very fine scale and could be applied to specific questions (e.g., Szép et al. 2003, Morrissey et al. 2004, Donovan et al. 2006). In summary, stable isotope analysis is a promising technique, but additional studies are required to refine the existing isotopic maps (especially for δD, $\delta^{18}O$, $\delta^{13}C$), develop and validate maps on more novel isotopes (strontium and lead), understand interannual and altitudinal variations, understand physiological mechanisms that can influence ratios, and finally produce taxonomically specific maps (Hobson 2003, 2005; Rubenstein and Hobson 2004; Wunder et al. 2005; Lott and Smith 2006).

Use of Bayesian analyses integrating prior knowledge of abundance data for assignment of migrants and wintering birds could potentially improve the accuracy of individual assignments of wintering birds to breeding locations (Royle and Rubenstein 2004). This method takes into account the variations in stable isotopes on the breeding grounds and breeding densities of birds and weights the assignments of individuals based on the relative numbers from these sources of data. We were unable to apply this approach, because of a lack of information on breeding population densities in large parts of the breeding range. If adequate density data for most of the northern yellow warbler breeding range could be obtained, the accuracy of assignments of wintering birds to breeding populations would possibly increase.

As an alternative for a species with partial breeding abundance data, we used a geographic-information-system-based assignment approach by overlaying genetic and isotopic contours. One weakness of this approach is that individuals are attributed to an isotopic region with certainty (i.e., no error), as opposed to a probabilistic approach that incorporates a measure of error (see Wunder et al. 2005, Norris et al. 2006). For example, birds with δD values close to a contour cutoff would arbitrarily be assigned to a region rather than to the neighboring region because there is an error associated with the stable isotope measurement and biological processes. Thirty-two birds among the 408 birds assigned to a region had a δD value ±2‰ unit of any of the iso-cline values. There were about as many birds assigned to the upper region ($n = 17$) as to the lower region ($n = 15$), which suggests that this bias in the assignments was very minor. Another potential problem is the assumption that the relationship between feather values of northern yellow warblers and rain during growing season is well known, constant, and identical across individuals. Stable hydrogen ratios can be influenced by individual diet (Lott et al. 2003), age (Wassenaar and Hobson 2000, Hobson et al. 2004, Meehan et al. 2003), altitude (Hobson et al. 2003), and intra-individual factors (Smith and Dufty 2005). We do not have evidence that δD values within stopover sites differed between age or sex classes (Boulet 2004).

We attempted to account for these issues by breaking up the δD isoclines into broad geographic categories (40‰ wide intervals), to which we assigned individuals on the basis of their values. This assignment of individuals into broad categories takes into account errors in the kriging technique and bird estimate of the δD, though not in as statistically elegant a way as in other methods (Wunder et al. 2005, Norris et al. 2006). Because we are examining large-scale patterns in a species with continent-wide distribution, we feel confident that a more fine-scale and probabilistic approach would not alter our general conclusions, and that small deviations from the assumptions will not have a large effect on our results. Even using this relatively crude approach, we were able to gain novel insights about migration patterns and connectivity in the northern yellow warbler.

An additional issue that needs to be addressed in the future is the availability of statistical methods and software to assign individuals to regions based on very distinct types of data (i.e., DNA markers, stable isotope ratios, trace element values, and phenotypic data). We encourage the development of assignment and exclusion test programs, such as those developed for AFLP and microsatellite data (Duchesne and Bernatchez 2002, Piry et al. 2004). These two programs include simulation tools to assess the quality of the assignments.

Migration Systems: Why Do Northern Yellow Warblers Migrate the Way They Do?

The northern yellow warbler has a complex migration system. The eastern and western lineages clearly exhibit a parallel migration system with slight overlapping of the lineages. A central question that remains to be answered is whether eastern and western lineages co-occur in South America and, if so, where and in what proportions. Depending on whether the distribution of western haplotypes extends down to South America or not, the parallel migration system corresponds to Salomonsen's (1955) pattern VIII (lineages have the same average wintering latitude) or pattern IX (average latitude of eastern lineage located farther south). On the other hand, the distribution of the highly migratory lineages (eastern and western) versus the distribution of the southern lineage suggests a leap-frog migration pattern, where the highly migratory lineages overshoot the breeding and wintering grounds of the southern lineage (migration pattern XIV; Salomonsen 1955). Our preliminary results certainly call for additional sampling on the wintering grounds, especially in South America, to better delineate the wintering range of the eastern and western lineages. Below, we discuss some possible reasons for the occurrence of these complex patterns.

Historical factor: Pleistocene glaciations.— Because of its temperate-to-boreal breeding distribution, the northern yellow warbler was greatly influenced by the Pleistocene glaciations (Milot et al. 2000, Boulet and Gibbs 2006). During the maximum extent of glaciation, the breeding grounds of wood warblers were reduced and shifted southward to at least 40°N latitude in eastern North America and 45°N latitude in western North America. The eastern refuge was likely located in the southeastern United States, though some habitats were possibly present on the exposed George Bank and the Glacial Islands (Williams and Webb 1996, Boulet and Gibbs 2006). In the western lineage, there is some evidence for a single refugium located in the vicinity of the pluvial lakes in west North America (Boulet and Gibbs 2006). Thus, the lineages became isolated during glaciation and probably had distinct and non-overlapping migration routes and wintering grounds. For example, the eastern lineage could have wintered in South America and the western lineage in Mexico according to the genetic contours. After the ice retreated, the lineages expanded and finally met in central North America, resulting in the actual overlap in their annual distributions. Using simulations of wind patterns and reconstruction of available breeding habitats, Williams and Webb (1996) demonstrated that the actual general heading of birds migrating over eastern North America in fall (155°) would have functioned 18,000 years ago during the Wisconsin maximum glaciation. The trans-Gulf and trans-Atlantic routes were possibly less risky at that time. First, wind patterns were more favorable for a southeastern migration than now. Second, the increase in emerged land in the Gulf of Mexico resulting from lower water levels provided a series of stopover habitats for birds on their way to Central and South America. For the western lineage, simulations indicate that wind patterns at 18,000 years before present were favorable for overland migration along the western and Pacific migration routes. As the western lineage expanded eastward on the breeding and wintering grounds, some individuals probably switched to a circum-Gulf route to reduce the energetic costs of migration. The observed routes taken by the eastern and western lineages thus likely have a historical component.

The presence of an east–west winter divide in five other Nearctic–Neotropical migrant species (Smith et al. 2005) indicates that these species were likely influenced by the same historical event (Avise 2004). For Swainson's Thrush, Ruegg and Smith (2002) argued that the circuitous migration observed in the continental lineage (which breeds from eastern Canada up to Alaska and winters in South America) is an artifact of the Pleistocene glaciations, whereby birds are retracing their historical route of expansion instead of using a more direct route. However, other ecological factors can come into play to explain some migration detours, such as winds, weather, stopover quality, facility in regaining fat reserves, predation, etc. (Alerstam 2001). For example, the favorable winds blowing over the Atlantic are of prime importance for explaining the circuitous trans-Atlantic route taken by the Blackpoll Warbler (*D. striata*) during fall migration (Nisbet 1970, McNair and Post 1993, Baird 1999; but see Murray 1989). Similarly, wind patterns in North America may have a significant role in the circuitous migration system of continental Swainson's Thrush (see below).

Ecological factors: Migration costs and competition.—Lundberg and Alerstam (1986) proposed a model to explain the development and maintenance of a parallel migration system as observed in the eastern and western lineages. Their simulation model had 32 breeding sites and two wintering populations from distinct areas (populations I and II). Wintering population II was located slightly farther away but had three times more resources. They incorporated three factors: (1) migration costs, which were proportional to the straight-line distance between breeding and wintering sites; (2) asymmetric winter competition favoring individuals from the nearest breeding areas, because they can arrive first to the wintering sites; and (3) asymmetric breeding competition favoring individuals from the nearest wintering areas, because they can arrive first to the breeding sites. Thus, birds with the shortest migratory distances had a selective advantage, because of lower migratory costs and earlier arrival on breeding and wintering grounds. Significant migratory costs and asymmetric winter competition produced longitudinal segregation on breeding sites with a sharp divide between wintering populations I and II, because these factors favored birds with the shortest migration distance from nearest breeding sites. With asymmetric breeding competition, a sharp divide between populations I and II was obtained on the breeding sites when the resources for reproduction among the two breeding areas were similar. Otherwise, a large hybrid zone occupied by individuals from wintering populations I and II was obtained next to a zone dominated by individuals from wintering population II. Analogous results were obtained when the opposite situation was modeled (longitudinal winter segregation from two major breeding populations I and II).

These simulation results may help explain the wide winter divide present in the northern yellow warbler. As demonstrated by the migration patterns (Fig. 5), the western lineage migrates over shorter distances than the eastern lineage, implying differential migratory costs and possible asymmetric competition favoring the western lineage in central North America. In the northern yellow warbler, the winter divide was relatively wide (~1,250 km), which suggests possible minor differences in the carrying capacity of eastern and western breeding grounds. The western breeding grounds are more extended: they reach higher latitudes (Alaska, Yukon, Northwest Territories) because of milder climate conditions in western North America. In other species, partial to complete longitudinal segregation patterns were observed in Mexico or Central America. These include a diffuse divide attributable to partial mixing of Wilson's Warbler (Kimura et al. 2002) and Nashville Warbler (*Vermivora ruficapilla*; Lovette et al. 2004) or a sharp (<500 km) divide between the Yellow-breasted Chat (*Icteria virens*; Lovette et al. 2004) and Swainson's Thrush (Ruegg and Smith 2002). Thus, relative factors such as location of the annual range, distance between the breeding and the wintering grounds of specific lineages, or the carrying capacity of lineage habitats may modulate the sharpness of the divide and its location in relation to the lineage distributions.

We have some evidence that the southern lineage exhibited a leap-frog pattern in relation to the highly migratory eastern and western lineages. Additional sampling on the breeding and wintering grounds is required to verify this pattern. However, we do not expect the presence of southern birds in South America. Southern birds probably belong to *D. p. sonorana*, a distinctively bright yellow subspecies breeding in the southwestern United States and northern Mexico and wintering in Mexico and Central America (Bent 1963). In addition, *D. p.*

sonorana does not have as pointy wings as the other migratory subspecies, like *D. p. aestiva* and *D. p. amnicola* (Wiedenfeld 1991, Lowther et al. 2000). Leap-frog migration has been identified in several species on the basis of plumage variation of subspecies (Swarth 1920, Salomonsen 1955, Pienkowski et al. 1985, Boland 1990) and, recently, stable hydrogen ratios (Kelly et al. 2002, Clegg et al. 2003). Theoretical models suggest that leap-frog patterns are promoted by asymmetric competition through prior occupancy on breeding grounds alone or also on wintering grounds (i.e., already established individuals exclude individuals arriving later from best sites) as well by non-negligible migration costs (Lundberg and Alerstam 1986, Holmgren and Lundberg 1993). Under the "asymmetric competition through body size" hypothesis (i.e., large individuals exclude smaller individuals from best wintering sites), leap-frog migration can also develop if migration costs are low (Holmgren and Lundberg 1993). In Arizona, the subspecies *D. p. sonorana* (likely the southern lineage) migrates before *D. p. rubiginosa* (western lineage) and *D. p. amnicola* (western and possibly eastern lineage) (Phillips et al. 1964). Regarding body size, the northern yellow warblers breeding in the southwestern United States are larger than those breeding in northern areas (Dunn and Garrett 1997). The leap-frog pattern may therefore evolve under one or the other model, depending on the importance of migratory costs. We presume that the costs are not greatly elevated, given the absence of major barrier to migration, especially in the southern lineage. In the latter case, the model incorporating asymmetric competition via body size would be more plausible. This hypothesis makes sense, considering that the highly migratory eastern and western lineages differentiated from the less migratory southern lineage during the Pleistocene period, possibly when northern habitats became available as ice sheets receded (Boulet and Gibbs 2006).

Abiotic factors: Wind patterns.—Winds have a strong effect on migration patterns: without the assistance of winds, several Nearctic–Neotropical migrant species would not be able to cross the Gulf of Mexico (Gauthreaux and Belser 1999). Thus, it is not surprising that some passerine species show behavioral selection in terms of wind direction and weather conditions when initiating departure (Able 1973). Individuals able to select favorable wind conditions and the most profitable flight altitude would have a selective advantage: increased survival during migration and early arrival on breeding or wintering grounds with more fat reserves. This is particularly important, because individuals arriving earlier on breeding grounds tend to have higher reproductive success than individuals arriving later (Møller 1994, Lozano et al. 1996, Hasselquist 1998).

Wind patterns, by influencing migratory routes taken by birds, may partly maintain strong longitudinal connectivity at a continental scale (i.e., longitudinal segregation between lineages in the case of the northern yellow warbler). In North America, the relationship between global wind circulation, topography, and nocturnal migration of passerines over North and Central Americas is particularly striking. In spring, the mean directions of passerine migration (measured directly or by radar) are in agreement with the average directions of air flow at 500 m in altitude (Gauthreaux 1980). Briefly, at 20°N latitude (Yucatan, West Indies, Great Antilles), the migratory direction is west-northwest and northwest, and winds over the Gulf of Mexico are generally very favorable for a trans-Gulf migration, especially as the spring season progresses (Gauthreaux and Belser 1999). Then, migrating birds shift to a more northerly direction once in Florida and over the northeast coast of Mexico. Over the eastern part of the continent, the direction of migration is northeast or east-northeast, whereas in central North America, migration proceeds northward but bifurcates in the Great Lakes area, such that some passerines fly northwest toward the Prairies and others fly northeast toward eastern Canada. The genetic and isotopic markers suggest that eastern birds use a trans-Gulf migration route in spring, either crossing the western part of the Gulf (Stevenson 1957) or flying directly from the Yucatan Peninsula to Louisiana and Alabama (Bent 1963, Imholf 1976, Moore et al. 1990). The northeast and east-northeast winds in eastern North America can easily bring eastern birds to eastern Canada, a pattern also suggested by the similarity between Louisiana and Braddock Bay and by the banding record maps (Fig. 13–14). Eastern and western birds using the circum-Gulf route from Mexico (Fig. 12A) can take advantage of the northwest winds blowing over interior North America to reach the Canadian Prairies. In addition to historical expansions, these wind patterns could partly explain the northwestern stretch in the distribution of several species breeding in eastern North America, such as the Blackburnian Warbler (*D. fusca*), Cape May Warbler (*D. tigrina*), Blackpoll Warbler, Northern Waterthrush (*Seiurus noveboracensis*), and Blue-headed Vireo (*Vireo solitarius*), to name a few (Sibley 2000). Wind patterns over the Rocky Mountains and the Pacific coast are not as favorable for a north or northwest migration (Gauthreaux 1980), but migration directions shows northwestern movements concordant with the western route taken by western birds passing through Nevada and possibly New Mexico (Fig. 12A).

In the fall, there is less agreement between wind patterns and directional tendencies of nocturnal birds, especially in the central United States and in Florida (Gauthreaux 1980). Winds blow in the favorable southwest direction mostly south of Virginia, and mainly in unfavorable directions in the central United States. Nevertheless, east of the Appalachians, migratory movements follow the Atlantic coast and the mountains down to the Gulf of Mexico or through Florida, whereas west of the Appalachians, migration is directed southeast and south-southeast to the Atlantic coast. In the Prairies, winds are concordant with the general tendency of birds to fly in a southeasterly direction (Gauthreaux 1980). In the fall, there is strong evidence that eastern birds use the trans-Gulf route (Fig. 12B). However, the overall less-negative stable isotope ratios obtained in Fort Morgan, Alabama, than in Louisiana suggest that eastern birds from southerly breeding regions (i.e., the eastern United States) are missing from our data. We suggest two nonexclusive hypotheses for these missing birds: (1) they migrate through another area in the fall, such as Florida (Crawford and Stevenson 1984, Duncan and Weber 1985, Dunn and Garrett 1997) or over the western part of the Atlantic (Amos 1991) as does the Blackpoll Warbler (Baird 1999); or (2) these migrants migrated very early (e.g., as early as July; Lowther et al. 1999), and they were already gone when banding season started. In the Prairies, the southeast winds may benefit northern yellow warblers breeding in the overlap zone. However, the north-central United States is dominated by western birds, as shown by the eastward shift of the 50% fall migration contour (Fig. 4). Western birds mainly opt for the western and circum-Gulf migration routes, but a few may opt for the trans-Gulf route (Fig. 12B). In summary, wind patterns may modulate which routes will be used primarily by the lineages during spring and fall migration on a short time scale. It would be interesting to simulate the effects of winds on the distribution of northern yellow warbler migrants in general and on the spring and fall distributions of the lineages specifically. We suspect that wind patterns may displace birds and this explains the presence of eastern birds in western North America and western birds in eastern North America.

EVOLUTIONARY ASPECTS: GENETIC CONTROL OF THE MIGRATION SYSTEM?

Migratory behavior, timing of initiation of migration, and migratory direction have a genetic basis (Berthold et al. 1990, 1992; Helbig 1992; Berthold 1996, 2001; Pulido et al. 2001). This raises the question: do birds of the eastern, southern, and western lineages have a different genetic migration program? Migratory activity is believed to be controlled by the same few nuclear genes that determine migratory and residency behavior (Berthold 2001). The migration patterns illustrated in Figure 5 (or see data in Table 1) and the overall distributions on lineages (Figs. 1–4) suggest that mitochondrial lineages may exhibit different levels of migratory activity: on average, southern birds migrated over shorter distances, whereas eastern and western birds migrated over greater distances. In the case of the southern versus eastern and western lineages, the differences in migratory distances parallel changes in the shape of the wings, which suggests not only genetic but also morphological adaptative differences for increased migratory behavior (Wiedenfeld 1991).

The average directions of movements over the United States are largely concordant with the pathways summarized by the multivariate analysis. In reality, individual pathways are probably composed of a series of vectors and may vary among individuals (Berthold 2001). In the overlap zone, judging from banding data, most birds had northwest–southeast headings (between 113° and 139°) but some had north-northwest–south-southeast headings (between 167° and 174°). If the migratory direction is under genetic control (assuming that nuclear genes are structured like the mitochondrial marker), birds should have headings between the average headings of eastern (east-northeast–west-southwest, northeast–southwest) and western birds (northwest–southeast), that is, more southerly headings and not headings typical of the western zone (Helbig 1992). We suggest two nonexclusive hypotheses: (1) finer-scale genetic differences between populations better explain the diverse directions observed in northern yellow warblers; and (2) the headings in North America may be constrained by additional factors, such as wind patterns (Gauthreaux 1980).

Evolutionary Aspects: Lineage-specific Migratory Strategies?

If southern birds are short-distance migrants, traveling <3,000 km per seasonal migration, most eastern and western birds are long-distance migrants. Nevertheless, birds belonging to the eastern and western lineages probably have different migratory strategies and physiological preparation determined by the migration routes they may use (i.e., western or circum-Gulf route vs. trans-Gulf route). Opting for the trans-Gulf route implies a 15- to 20-h nonstop flight over a large body of water. Favorable winds and high fat loads are essential for a successful flight (Gauthreaux and Belser 1999). When weather conditions over the Gulf of Mexico are unfavorable (strong rain, adverse winds, storms), some birds barely make it to the first available land or offshore oil rigs, but many probably die *en route* or once on stopover (Gauthreaux 1999, Moore 2000). With global warming, breeding populations from eastern North America using the trans-Gulf route may be at higher risk because of unfavorable weather conditions over the Gulf of Mexico from climatic disturbances and an increase in the frequency and severity of tropical storms and hurricanes (Gray 1993, NOAA 2005). By contrast, birds using the circum-Gulf route may more easily find a safe stopover to replenish their fat reserves when weather conditions are not favorable. They may not need to carry high fat loads, because they can stop at several stopovers during migration (Alerstam 2001).

Another difference between the circum-Gulf and trans-Gulf routes is the number of daily steps to reach the breeding grounds. When crossing the Gulf, birds depart at night and keep flying until they reach land the next day, usually in the afternoon. By contrast, birds migrating overland stop flying long before daylight. A bird departing from the Yucatan Peninsula would reach the northern coast of the Gulf of Mexico five or six days later (Gauthreaux 1999). It would be interesting to determine whether eastern birds arrive earlier than western birds on territories in the overlap zone, as they tend to do on stopovers (Boulet 2004), and whether this leads to a difference in their mating and reproductive successes. The survival rate on a circum-Gulf route may be higher than that on a trans-Gulf route, especially for hatch-year birds in fall and second-year birds in spring. However, birds taking the circum-Gulf route may be more susceptible to predation when they spend daylight hours in unfamiliar stopovers habitats.

We detected flyways used by the eastern and western lineages by analyzing genetic and δD data for a small number of stopovers. Limited range of sampling days may have biased some of our results because we missed early or late migrants. In particular, Bosque del Apache was sampled over 17 days in spring and 14 days in fall. In spring, mean δD value was higher than in other stopovers, whereas in fall, mean δD value was comparable with the value in Glenn and Tehama counties. If early or late migrants are missing from the data sets, the "distinct" flyway observed at Bosque del Apache in spring may be an artifact. For fall migration in 1998, there is evidence that northern yellow warblers migrated before and after our dates of sampling (Kelly 2006). However, range of δD values was higher in our study (range: 76, n = 43 individuals) than in Kelly's (2006) study (range: 62, n = 18 individuals), even if our sampling period was one-third of Kelly's (2006) sampling period. Additional sampling over extended periods (at least three weeks) and repeated sampling over years would refine flyway patterns and assess their stability, especially if they are derived from stable isotope data alone. In the long term, we believe that additional data should be collected across many more stopovers to better delineate the flyways used by distinct groups and understand how birds use the landscape during migration.

Conservation Implications of Migration Patterns

Several migratory species show regional to large-scale declines in North America (Robbins et al. 1989, Sauer et al. 2004). Knowing where the declining breeding populations overwinter would help long-term conservation plans, because biologists would be able to determine whether the causes of the decline are specific to the breeding grounds, the wintering grounds, or both. On the basis of studies of DNA variation (mostly mtDNA but also microsatellites) and stable isotope analyses (mostly stable hydrogen), the general pattern emerging in Nearctic–Neotropical migrant species with very broad longitudinal breeding ranges is strong continental-scale connectivity and weak-to-absent regional-scale connectivity (Kimura et al. 2002, Ruegg and Smith 2002, Clegg et al. 2003, Lovette et al. 2004). The similar levels of connectivity across species may simply be attributable to the common level of resolution of the markers used in these different studies. However, if the use of additional markers confirms the pattern of strong large-scale connectivity and weak regional-scale connectivity, it would mean that individuals from a given regional breeding area mix with individuals from other breeding areas on the wintering grounds and stopovers, and vice versa. The degree of connectivity observed within the eastern-lineage northern yellow warbler may apply to Nearctic–Neotropical migrant species with smaller breeding ranges, such as the Cerulean Warbler (*D. cerulea*), Hooded Warbler (*W. citrina*), Black-throated Warbler, and Wood Thrush (*Hylocichla mustelina*)—if these species indeed share a common history with the eastern lineage. In the event that future research confirms the weak-to-absent "regional-scale connectivity" hypothesis, local populations would be less vulnerable to stochastic events and habitat changes on their breeding or wintering grounds, because any adverse effects would be dispersed over several populations. This degree of connectivity would be a key feature buffering migratory species against extinction during stochastic perturbations and climatic changes, and migratory species may persist longer than nonmigratory species (Helbig 2003).

Another step is to determine whether the parallel migration system found in the northern yellow warbler can be found in other species with similar or less-extended breeding and wintering ranges. The finding of concordant phylogeographic patterns among migratory species (i.e., aspect III of genealogical concordance; Avise 2000) on breeding and wintering grounds signifies that conservationists could adopt large-scale multispecies management plans rather than single-species plans, as has been done for migratory waterfowl. For example, Lincoln (1935) defined four migration flyways in North America based on a large-scale analysis of banded waterfowl: the Atlantic, Mississippi, Central, and Pacific flyways. Later, governmental agencies adopted these flyways as administrative units (Hawkins et al. 1984) for managing populations and setting hunting regulations. The main objective in the assessment of migratory connectivity is to identify the habitats used by differentiated sets of populations throughout the annual cycle. Now that we have uncovered concordant connectivity patterns among several passerine species (e.g., Yellow Warbler, Wilson's Warbler, Swainson's Thrush), we can go beyond the migratory connectivity concept and envisage managing species by "phylogeographic" flyways and set conservation objectives accordingly. Taking the northern yellow warbler as a model, three phylogeographic flyways could be defined: (1) the zone annually used mainly by the eastern lineage, (2) the zone annually used mainly by the western lineage, and (3) the zone annually used by both lineages, because we cannot currently distinguish them in the field. Such zones could be defined with the help of geostatistical techniques based on range distributions of distinct groups. Population trends could be analyzed by lineage for each of the main seasons (breeding, fall migration, wintering, and spring migration) when such data are available. A network of stopovers could be identified within phylogeographic flyways to ensure that populations can accomplish their annual cycle. Adopting this approach would possibly simplify conservation plans, because conservation efforts would be coordinated for species belonging to the same guilds and influenced by the same historical factors. However, distributions of distinct groups may not be well defined, and some groups or populations could cross from one flyway to another. Before adopting this kind of approach, we need to verify whether there is no strong fine-scale connectivity in Nearctic–Neotropical migrants. If diffuse fine-scale connectivity exists, flyways could possibly be further subdivided into smaller units.

ACKNOWLEDGMENTS

During the course of this work, we contacted many people working throughout the Americas to obtain samples from breeding, migratory, and overwintering Yellow Warblers. We want thank the following people and institutions for help with sample collection, for without their dedicated assistance, this project would not have been possible: R. Ludkin, L. Mousseau, J. Smith, J. Miles, J. Farrington, F. Moore, E. Paxton, K. B. Burk, K. Voget, M. Grosselet, O. Cruz, J. Woods, A.-M. Barber, T. Pogson, A. Solomon, Point Reyes Bird Observatory (R. Geupel and M. Flannery), S. L. Jones, S. H. Craig, D. A. Cohrs, C. Pitman, J. Carlisle, J. C. Owen, H. den Haan, S. Yezerinac, R. Keith, D. Flath, G. Taylor, D. L. Swanson, J. MacKay, E. M. Ammon, J. Lytle, R. Dawson, E. Milot, N. Wheelwright, R. P. Yunick, D. M. Finch, J. Kelly, S. Cox, H. Walker, E. W. Brooks, D. Bonter, B. Milá, S. S. Mitra, I. Paterson, M. C. Shieldcastle, A. Chartier, B. Hall-Brooks, D. P. Vroman, R. C. Leberman, R. S. Mulvihill, G. W. Lasley, D. Connel, K. A. Arnold, J. Massey, F. Collins, J. Banta, J. Graham, K. Baer, R. C. Simpson, M. Whitfield, and any other banders and volunteers who may have plucked feathers for this project. We give special thanks to J. Hinshaw at the Bird Division, Museum of Zoology, University of Michigan, for her help with feather importation.

In addition, we want to thank the following individuals for providing access to museum samples under their care: R. Zink at the Bell Museum, University of Minnesota in Minneapolis; S. Calmé at ECOSUR in Chetumal; P. Escalante Pliego at the Universidad Nacional Autónoma de México (UNAM) in Mexico City; A. Navarro Siguenza at UNAM in Mexico City; J. Vargas Soriano at CEDESU–Universidad Autónoma de Campeche in Campeche; the Laboratorio de Investigacion en Ornitologia at Universidad Michoacana de San Nicolas de Hildago; S. S. Arriega-Weiss at the Departamento de Biologia of Universidad Juárez Autónoma de Tabasco in Villahermosa; E. Quiroz of the Instituto Conmemorativo Gordas de Estudios de la Salud (Gordas Memorial Museum) in Panama City; and A. Baker at the Royal Ontario Museum in Toronto. We extend a special thanks to T. Smith at the Center for Tropical Research, University of California at Los Angeles, for providing substantial numbers of DNA samples collected under his supervision.

In Mexico, field and logistic assistance was provided by S. Calmé, M. SanVincente Lopez, F. Durand Siller, M. A. Plata Made, A. Vallejos Sánchez, L. Hernández Puch, and Chucho in Celestun, C. Vargas (SEMARNAP), S. S. Arriega-Weiss and his students (C. M. Jiménez, A. Ibarra Macias, T. F. Díaz Thompson, G. Alejandro Arias, J. Hernández de la Cruz, and D. E. Alonzo Parra) and the people at the DUMAC station in Celestun. Special thanks to D. Buehler, A. I. Castillo and his family, L. A. Ríos (Fertica, Chiriquí), M. Leone, G. Angher and E. Bermingham at the Smithsonian Tropical Research Institute in Panama. These people all provided invaluable assistance during the Panama trip.

We express our sincere gratitude to L. De Sousa for laboratory assistance, as well as to N. Bulgin, R. Pearce, L. M. Tabak, and P. Healy. We thank P. Petitclerc for assistance with geostatistical and banding analyses and S. Dudley for assistance with statistical analyses. Comments from R. Robertson, S. Balshine, J. Faaborg, M. Wunder, and L. Eggert improved the manuscript.

Funding for this work was provided by Natural Sciences and Engineering Research Council (NSERC) grants and a Premier's Research Award to H.L.G. and Max Bell Foundation and STAGE (Environment Canada) grants to H.L.G. and K.A.H. M.B. was supported by fellowships from NSERC, FQRNT, OGSST, and the Department of Biology at McMaster University. M.B. is particularly grateful to the Department of Biology at McMaster University for providing financial support during the last months of thesis writing.

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.

AGRESTI, A. 1996. An Introduction to Categorical Data Analysis. John Wiley and Sons, New York.

ALERSTAM, T. 2001. Detours in bird migration. Journal of Theoretical Biology 209:319–331.

AMOS, E. J. R. 1991. A Guide to the Birds of Bermuda. Warwick, Bermuda.

AVISE, J. C. 2000. Phylogeography: The History and Formation of Species. Harvard University Press, Cambridge, Massachusetts.

AVISE, J. C. 2004. Molecular Markers, Natural History, and Evolution, 2nd ed. Sinauer Associates, Sunderland, Massachusetts.

BAILEY, T. C., AND A. C. GATRELL. 1995. Interactive Spatial Data Analysis. John Wiley and Sons, New York.

BAIRD, J. 1999. Returning to the tropics: The epic autumn flight of the Blackpoll Warbler. Pages 63–76 *in* Gatherings of Angels: Migrating Birds and Their Ecology (K. P. Able, Ed.). Comstock Books, Ithaca, New York.

BEARD, B. L., AND C. M. JOHNSON. 2000. Strontium isotope composition of skeletal material can determine the birth place and geographic mobility of humans and animals. Journal of Forensic Science 45:1049–1061.

BENSCH, S., S. ÅKESSON, AND D. E. IRWIN. 2002a. The use of AFLP to find an informative SNP: Genetic differences across a migratory divide in Willow Warblers. Molecular Ecology 11: 2359–2366.

Bensch, S., T. Andersson, and S. Åkesson. 1999. Morphological and molecular variation across a migratory divide in Willow Warblers, *Phylloscopus trochilus*. Evolution 53:1925–1935.

Bensch, S., A. J. Helbig, M. Salomon, and I. Seibold. 2002b. Amplified fragment length polymorphism analysis identifies hybrids between two subspecies of warblers. Molecular Ecology 11:473–481.

Bent, A. C. 1963. Life Histories of North American Wood Warblers. Dover, New York.

Berthold, P. 1996. Control of Bird Migration. Chapman and Hall, London.

Berthold, P. 2001. Bird Migration: A General Survey, 2nd ed. Oxford University Press, London.

Berthold, P., A. J. Helbig, G. Mohr, and U. Querner. 1992. Rapid microevolution of migratory behaviour in a wild bird species. Nature 360:668–670.

Berthold, P., W. Wiltschko, H. Miltenberger, and U. Querner. 1990. Genetic transmission of a migratory behavior into a nonmigratory bird population. Experientia 46:107–108.

Boland, J. M. 1990. Leapfrog migration in North American shorebirds: Intra- and interspecific examples. Condor 92:284–290.

Boulet, M. 2004. Evolutionary history and migration patterns in the Yellow Warbler (*Dendroica petechia*). Ph.D. dissertation, McMaster University, Hamilton, Ontario.

Boulet, M., and H. L. Gibbs. 2006. Lineage origin and expansion of a Neotropical migrant songbird after recent glaciation events. Molecular Ecology 15:2505–2525.

Boulet, M., and D. R. Norris. 2006. The past and present of migratory connectivity. Pages 1–13 *in* Patterns of Migratory Connectivity in Two Nearctic–Neotropical Songbirds: New Insights from Intrinsic Markers (M. Boulet and D. R. Norris, Eds.). Ornithological Monographs, no. 61.

Boulet, M., C. Potvin, F. Shaffer, A. Breault, and L. Bernatchez. 2005. Conservation genetics of the threatened Horned Grebe (*Podiceps auritus* L.) population of the Magdalen Islands, Québec. Conservation Genetics 6:539–550.

Brewer, D., A. Diamond, E. J. Woodsworth, B. T. Collins, and E. H. Dunn. 2000. Canadian Atlas of Bird Banding. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario.

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

Buehler, D. M. 2003. Phylogeography and genetic diversity in Red Knots (*Calidris canutus*). M.Sc. thesis, University of Toronto, Toronto, Ontario.

Bulgin, N. L., H. L. Gibbs, P. Vickery, and A. J. Baker. 2003. Ancestral polymorphisms in genetic markers obscure detection of evolutionarily distinct populations in the endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*). Molecular Ecology 12: 831–844.

Caccamise, D. F., L. M. Reed, P. M. Castelli, S. Wainright, and T. C. Nichols. 2000. Distinguishing migratory and resident Canada Geese using stable isotope analysis. Journal of Wildlife Management 64:1084–1091.

Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. Feng, T. W. Sherry, and G. R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecologia 109: 132–141.

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.

Crawford, R. L., and H. M. Stevenson. 1984. Patterns of spring and fall migration in northwest Florida. Journal of Field Ornithology 55: 196–203.

Donovan, T., J. Buzas, P. Jones, and H. L. Gibbs. 2006. Tracking dispersal in birds: Assessing the potential of elemental markers. Auk 123: 500–511.

Duchesne, P., and L. Bernatchez. 2002. AFLPOP: A computer program for simulated and real population allocation, based on AFLP data. Molecular Ecology Notes 2:380–383.

Duchesne, P., C. Étienne, and L. Bernatchez. 2006. PERM: A computer program to detect structuring factors in social units. Molecular Ecology Notes 6: in press.

Dugger, K. M., J. Faaborg, W. J. Arendt, and K. A. Hobson. 2004. Understanding survival and abundance of overwintering warblers: Does rainfall matter? Condor 106:744–760.

Duncan, R. A., and W. E. Weber. 1985. The Yellow Warbler: A diurnal circum-Gulf fall migrant. Florida Field Naturalist 13:20–22.

Dunn, J. L., and K. L. Garrett. 1997. Peterson Field Guide to Warblers of North America. Houghton Mifflin, New York.

Esler, D. 2000. Applying metapopulation theory to conservation of migratory birds. Conservation Biology 14:366–372.

Gauthreaux, S. A., Jr. 1980. The influence of global climatological factors on the evolution of bird migratory pathways. Pages 517–525 *in* Acta XVII Congressus Internationalis Ornithologici

(R. Nöhring, Ed.). Deutsche Ornithologen-Gesellschaft, Berlin.

Gauthreaux, S. A., Jr. 1999. Neotropical migrants and the Gulf of Mexico: The view from aloft. Pages 27–48 *in* Gathering of Angels: Migrating Birds and Their Ecology (K. P. Able, Ed.). Comstock Books, Ithaca, New York.

Gauthreaux, S. A., Jr., and C. G. Belser. 1999. Bird migration in the region of the Gulf of Mexico. Pages 1931–1947 *in* Acta XXII Congressus Internationalis Ornithologici (N. J. Adams and R. H. Slotow, Eds.). BirdLife South Africa, Johannesburg.

Gibbs, H. L., R. J. G. Dawson, and K. A. Hobson. 2000. Limited differentiation in microsatellite DNA variation among northern populations of the Yellow Warbler: Evidence for male-biased gene flow? Molecular Ecology 9: 2137–2147.

Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412:436–438.

Gray, C. R. 1993. Regional meteorology and hurricanes. Pages 87–99 *in* Climatic Change in the Intra-Americas Sea: Implications of Future Climate on the Ecosystems and Socio-economic Structure in the Marine and Coastal Regions of the Caribbean Sea, Gulf of Mexico, Bahamas, and the Northeast Coast of South America (G. A. Maul, Ed.). Edward Arnold, London.

Haig, S. M., C. L. Gratto-Trevor, T. D. Mullins, and M. A. Colwell. 1997. Population identification of western hemisphere shorebirds throughout the annual cycle. Molecular Ecology 6:413–427.

Hasselquist, D. 1998. Polygyny in Great-reed Warblers: A long-term study of factors contributing to male fitness. Ecology 79:2376–2390.

Hawkins, A. S., R. C. Hanson, H. K. Nelson, and H. M. Reeves. 1984. Flyways: Pioneering Waterfowl Management in North America. U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C.

Helbig, A. J. 1992. Population differentiation of migratory directions in birds: Comparison between ringing results and orientation behaviour of hand-raised migrants. Oecologia 90: 483–488.

Helbig, A. J. 2003. Evolution of bird migration: A phylogenetic and biogeographic perspective. Pages 3–20 *in* Avian Migration (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Berlin.

Hobson, K. A. 2003. Making migratory connections with stable isotopes. Pages 379–392 *in* Avian Migration (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Berlin.

Hobson, K. A. 2005. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. Auk 122:1037–1048.

Hobson, K. A., Y. Aubry, and L. I. Wassenaar. 2004. Migratory connectivity in Bicknell's Thrush: Locating missing populations with hydrogen isotopes. Condor 106:905–909.

Hobson, K. A., K. P. McFarland, L. I. Wassenaar, C. C. Rimmer, and J. E. Goetz. 2001. Linking breeding and wintering grounds of Bicknell's Thrushes using stable isotope analyses of feathers. Auk 118:16–23.

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. 2001. Isotopic delineation of North American migratory wildlife populations: Loggerhead Shrikes. Ecological Applications 11:1545–1553.

Hobson, K. A., L. I. Wassenaar, B. Milá, L. Lovette, C. Dingle, and T. B. Smith. 2003. Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. Oecologia 136:302–308.

Hobson, K. A., L. I. Wassenaar, and O. R. Taylor. 1999. Stable isotopes (δD and δ^{13}C) are geographic indicators of natal origins of monarch butterflies in eastern North America. Oecologia 120:397–404.

Holmgren, N., and S. Lundberg. 1993. Despotic behaviour and the evolution of migration patterns in birds. Ornis Scandinavica 24:103–109.

Hosmer, D. W., Jr., and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley and Sons, New York.

Imholf, T. A. 1976. Alabama Birds, 2nd ed. University of Alabama Press, Tuscaloosa.

International Atomic Energy Agency (IAEA). 2001. Isotope hydrology information system (ISOHIS) database. [Online.] Available at isohis.iaea.org.

Jenness, J. 2002. PATH, WITH DISTANCES AND BEARINGS, version 3. Jenness Enterprise, Flagstaff, Arizona. [Online.] Available at www.jennessent.com.

Johnston, K., J. M. Ver Hoef, K. Krivoruchko, and N. Lucas. 2001. ARCGIS 9. Using ARCGIS Geostatistical Analyst. ESRI, Redlands, California.

Kelly, J. F. 2006. Stable isotope evidence links breeding geography and migration timing in wood warblers (Parulidae). Auk 123:431–437.

Kelly, J. F., and D. B. Finch. 1998. Tracking migrant songbirds with stable isotopes. Trends in Ecology and Evolution 13:48–49.

Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216–221.

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.

Kimura, M., S. M. Clegg, I. J. Lovette, K. R. Holder, D. J. Girman, B. Milá, P. Wade, and T. B. Smith. 2002. Phylogeographical approaches to assessing demographic connectivity between breeding and overwintering regions in a Nearctic–Neotropical warbler (*Wilsonia pusilla*). Molecular Ecology 11:1605–1616.

Klein, N. K., and W. M. Brown. 1994. Intraspecific molecular phylogeny in the Yellow Warbler (*Dendroica petechia*), and implications for avian biogeography in the West Indies. Evolution 48: 1914–1932.

Lincoln, F. C. 1935. The waterfowl flyways of North America. U.S. Department of Agriculture, circular no. 342.

Lott, C. A., T. D. Meehan, and J. A. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulphur stable isotopes in feathers: Influence of marine prey base. Oecologia 134:505–510.

Lott, C. A., and J. P. Smith. 2006. A geographic-information-system approach to estimating the origin of migratory raptors in North America using stable hydrogen isotope ratios in feathers. Auk 121:822–835.

Lovette, I. J., S. M. Clegg, and T. B. Smith. 2004. Limited utility of mtDNA markers for determining connectivity among breeding and overwintering locations in three Neotropical migrant birds. Conservation Biology 18:156–166.

Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector. 1999. Yellow Warbler (*Dendroica petechia*). *In* The Birds of North America, no. 454 (A. Poole and F. Gill, Ed.). Birds of North America, Philadelphia.

Lozano, G. A., S. Perreault, and R. E. Lemon. 1996. Age, arrival date, and reproductive success of male American Redstarts *Setophaga ruticilla*. Journal of Avian Biology 27:164–170.

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 by using stable-carbon isotopes. Science 282:1884–1886.

Marra, P. P., D. R. Norris, S. M. Haig, M. Webster, and J. A. Royle. 2006. Migratory connectivity. Pages 157–183 *in* Connectivity Conservation (K. Crooks and M. Sanjayan, Eds.). Cambridge University Press, New York.

Mazerolle, D. F., K. A. Hobson, and L. I. Wassenaar. 2005. Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of White-throated Sparrows at a migration monitoring station. Oecologia 144:541–549.

McNair, D. B., and W. Post. 1993. Autumn migration route of Blackpoll Warblers: Evidence from southeastern North America. Journal of Field Ornithology 64:417–425.

Meehan, T. D., C. A. Lott, Z. D. Sharp, R. B. Smith, R. N. Rosenfield, A. C. Stewart, and R. K. Murphy. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. Condor 103:11–20.

Meehan, T. D., R. N. Rosenfield, V. N. Atudorei, J. Bielefeldt, L. J. Rosenfield, A. C. Stewart, W. E. Stout, and M. A. Bozek. 2003. Variation in hydrogen stable-isotope ratios between adult and nestling Cooper's Hawks. Condor 105: 567–572.

Milá, B., D. J. Girman, M. Kimura, and T. B. Smith. 2000. Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. Proceedings of the Royal Society of London, Series B 267:1033–1040.

Milot, E., H. L. Gibbs, and K. A. Hobson. 2000. Phylogeography and genetic structure of northern populations of the Yellow Warbler (*Dendroica petechia*). Molecular Ecology 9:667–681.

Møller, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. Behavioral Ecology and Sociobiology 35: 115–122.

Moore, F. R., Ed. 2000. Stopover ecology of Nearctic–Neotropical landbird migrants: Habitat relations and conservation implications. Studies in Avian Biology, no. 20.

Moore, F. R., P. Kerlinger, and T. R. Simons. 1990. Stopover on a Gulf Coast barrier island by spring trans-Gulf migrants. Wilson Bulletin 102:487–500.

Morrissey, C. A., L. I. Bendell-Young, and J. E. Elliott. 2004. Linking contaminant profiles to the diet and breeding location of American Dippers using stable isotopes. Journal of Applied Ecology 41:502–512.

Murray, B. G., Jr. 1989. A critical review of the transoceanic migration of the Blackpoll Warbler. Auk 106:8–17.

National Oceanic and Atmospheric Administration (NOAA). 2005. NOAA: 2006 Atlantic hurricane outlook. [Online.] Available at www.cpc.ncep.noaa.gov/products/outlooks/hurricane.shtml.

Nisbet, I. C. T. 1970. Autumn migration of the Blackpoll Warbler: Evidence for long flight provided by regional survey. Journal of Field Ornithology 41:207–233.

Norman, G. R., and D. L. Streiner. 2000. Biostatistics: The Bare Essentials, 2nd ed. B. C. Decker, Hamilton, Ontario.

Norris, D. R., P. P. Marra, T. K. Kyser, J. A. Royle, G. J. Bowen, and T. M. Ratcliffe. 2006. Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). Pages 14–28 *in* Patterns of Migratory Connectivity in Two Nearctic–Neotropical Songbirds: New Insights from Intrinsic Markers (M. Boulet and D. R. Norris, Eds.). Ornithological Monographs, no. 61.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and T. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London, Series B 271:59–64.

Peach, W., S. Baillie, and L. Underhill. 1991. Survival of British warblers *Acrocephalus schoenobaenus* in relation to West African rainfall. Ibis 133:300–305.

Phillips, A. R., J. Marshall, and G. Monson. 1964. The Birds of Arizona. University of Arizona Press, Tucson.

Pienkowski, M. W., P. R. Evans, and D. J. Townshend. 1985. Leap-frog migration and other migration patterns of waders: A critique of the Alerstam and Hogstedt hypothesis, and some alternatives. Ornis Scandinavica 16:61–70.

Piry, S., A. Alapetite, J.-M. Cornuet, D. Paetkau, L. Baudouin, and A. Estoup. 2004. GENECLASS2: A software for genetic assignment and first-generation migrant detection. Journal of Heredity 95:536–539.

Pulido, F., P. Berthold, G. Mohr, and U. Querner. 2001. Heritability of the timing of autumn migration in a natural bird population. Proceedings of the Royal Society of London, Series B 268:953–959.

Ramos, M. A., and D. W. Warner. 1980. Analysis of North American subspecies of migrant birds wintering in Los Tuxtlas, southern Veracruz, Mexico. Pages 173–180 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.

Raveling, D. G., and D. W. Warner. 1978. Geographic variation of Yellow Warblers killed at a TV tower. Auk 95:73–79.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences USA 86:7658–7662.

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., C. P. Chamberlain, R. T. Holmes, M. P. Ayres, J. R. Waldbauer, G. R. Graves, and N. C. Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. Science 295:1062–1065.

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.

Ruegg, K. C., and T. B. Smith. 2002. Not as the crow flies: A historical explanation for circuitous migration in Swainson's Thrush (*Catharus ustulatus*). Proceedings of the Royal Society of London, Series B 269:1375–1381.

Salomonsen, F. 1955. The evolutionary significance of bird migration. Biologiske Meddelelser 22: 1–62.

Sauer, J. R., J. E. Hines, and J. Fallon. 2004. The North American Breeding Bird Survey, results and analyses 1966–2003, version 2004.1. [Online.] U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland. Available at www.mbr-pwrc.usgs.gov/bbs/bbs2003.html.

Seutin, G., B. N. White, and P. T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analysis. Canadian Journal of Zoology 69:82–90.

Sibley, D. A. 2000. The Sibley Guide to Birds. Knopf, New York.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288: 2040–2042.

Smith, A. D., and A. M. Dufty, Jr. 2005. Variation in the stable-hydrogen isotope composition of Northern Goshawk feathers: Relevance to the study of migratory origins. Condor 107: 547–558.

Smith, R. B., T. D. Meehan, and B. O. Wolf. 2003. Assessing migration patterns of Sharp-shinned Hawks *Accipiter striatus* using stable-isotope and band encounter analysis. Journal of Avian Biology 34:387–392.

Smith, T. B., S. M. Clegg, M. Kimura, K. C. Ruegg, B. Milá, and I. J. Lovette. 2005. Molecular genetic approaches to linking breeding and overwintering areas in five Neotropical migrant passerines. Pages 222–234 *in* Birds of

Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Stevenson, H. M. 1957. The relative magnitude of the trans-Gulf and circum-Gulf spring migrations. Wilson Bulletin 69:39–77.

Swarth, H. S. 1920. Revision of the avian genus *Passerella*, with special reference to the distribution and migration of the races in California. University of California Publications in Zoology, no. 21.

Szép, T., A. P. Møller, J. Vallner, B. Kovács, and D. Norman. 2003. Use of trace elements in feathers of Sand Martin *Riparia riparia* for identifying moulting areas. Journal of Avian Biology 34:307–320.

Tiedemann, R., K. B. Paulus, M. Scheer, K. G. von Kistowski, K. Skírnisson, D. Bloch, and M. Dam. 2004. Mitochondrial DNA and microsatellite variation in the Eider Duck (*Somateria mollissima*) indicate stepwise postglacial colonization of Europe and limited current long-distance dispersal. Molecular Ecology 13: 1481–1494.

Wassenaar, L. I., and K. A. Hobson. 2000. Improved method for determining the stable-hydrogen isotopic composition (δD) of complex organic materials of environmental interest. Environmental Science and Technology 34:2354–2360.

Wassenaar, L. I., and K. A. Hobson. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. Environmental Science and Technology 35:1845–1850.

Wassenaar, L. I., and K. A. Hobson. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes in Environmental and Health Studies 39:211–217.

Wassenaar, L. I., and K. A. Hobson. 2006. Stable-hydrogen isotope heterogeneity in keratinous materials: Mass spectrometry and migratory wildlife tissue sampling strategies. Rapid Communications in Mass Spectrometry 20: 1–6.

Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 *in* Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

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.

Wenink, P. W., and A. J. Baker. 1996. Mitochondrial DNA lineages in composite flocks of migratory and wintering Dunlins (*Calidris alpina*). Auk 113:744–756.

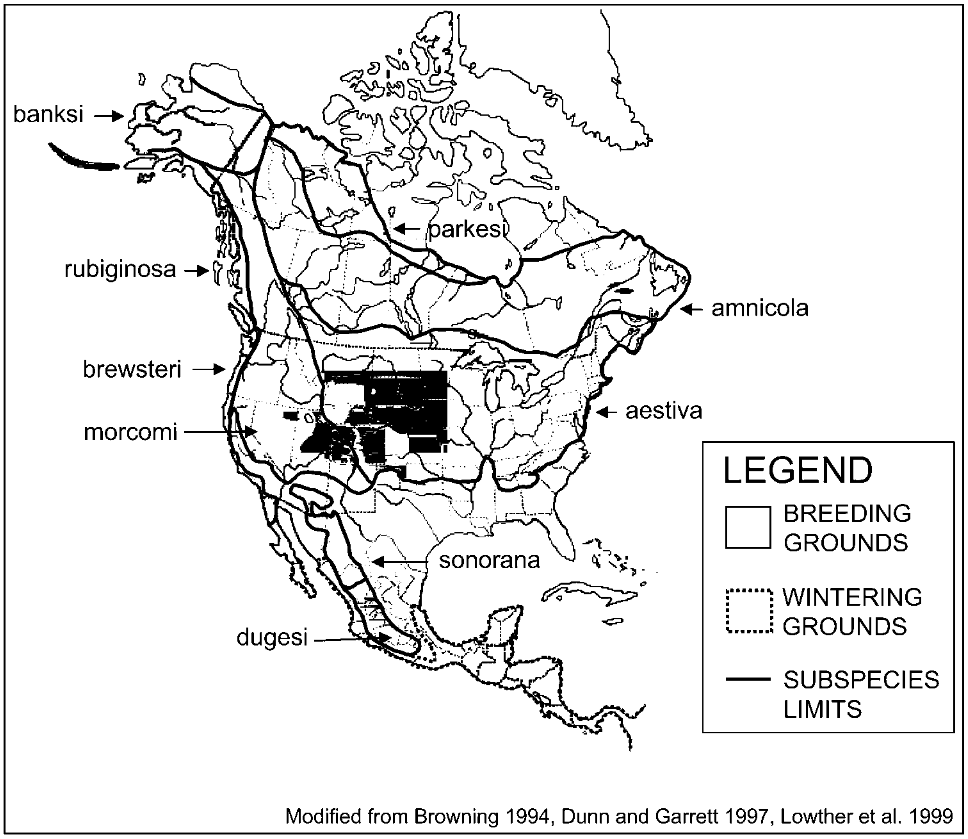
Wennerberg, L. 2001. Breeding origin and migration pattern of Dunlin (*Calidris alpina*) revealed by mitochondrial DNA analysis. Molecular Ecology 10:1111–1120.

Wiedenfeld, D. A. 1991. Geographical morphology of male Yellow Warblers. Condor 93:712–723.

Williams, T. C., and T. Webb III. 1996. Neotropical bird migration during the Ice Ages: Orientation and ecology. Auk 113:105–118.

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.

Appendix 1. Breeding and wintering ranges of the northern yellow warbler, the migratory form of the Yellow Warbler.



Modified from Browning 1994, Dunn and Garrett 1997, Lowther et al. 1999

Note that the wintering range of the northern yellow warbler extends to the northern part of South America (Columbia south to central Peru, northern Brazil, and Guyana). The corresponding breeding ranges of the nine northern yellow warbler species are delimited by solid lines. The Yellow Warbler also includes two resident forms: the golden warbler, from the West Indies and Florida; and the mangrove warbler, from coastal Mexico, Central America, and northern South America (ranges not shown).

Appendix 2. List of sampling sites included in the present study and their geographic coordinates (degree decimal). N_{seq} = number of sequenced individuals; N_{rsa} = number of individuals that were genotyped using region-specific PCR amplifications; and $N_{\mathrm{total}} = N_{\mathrm{seq}} + N_{\mathrm{rsa}}$. N_{total} is also east + west + south individuals. The identification number (ID) was used to label pie-charts in Figures 2–5.

Sampling sites	State or province	East	West	South	N_{total}	N_{seq}	N_{rsa}	Latitude (°N)	Longitude (°W)
Breeding sites (site ID)									
Bon Portage Island (1)	Nova Scotia, Canada	10	0	0	10	0	10	43.50	65.70
Braddock Bay (2)	New York, USA	10	0	0	10	5	5	43.31	77.71
Burnaby area (3)	British Columbia, Canada	0	13	0	13	6	7	49.25	122.70
Cape Breton (4)	Nova Scotia, Canada	8	0	0	8	5	3	46.17	60.75
Churchill (5)	Manitoba, Canada	10	14	0	24	22	2	58.73	94.12
Creston (6)[a]	British Columbia, Canada	0	26	0	26	26	0	49.10	116.50
Cuyahoga (7)	Ohio, USA	16	0	0	16	3	13	41.24	81.55
Deep Creek (8)	Wyoming, USA	1	6	0	7	5	2	42.72	109.01
Delta Marsh (9)[a]	Manitoba, Canada	26	1	0	27	27	0	50.20	98.20
Dodge Nature Center (10)	Minnesota, USA	2	0	0	2	2	0	44.98	93.26
El Paso County (11)	Colorado, USA	0	1	0	1	1	0	38.83	104.52
Fairbanks (12)[a]	Alaska, USA	0	11	0	11	11	0	64.84	147.72
Flagstaff (13)	Arizona, USA	0	3	3	6	6	0	35.20	111.65
Fletcher Lake (14)	British Columbia, Canada	0	8	0	8	8	0	51.67	123.00
Fort Riley (15)	Kansas, USA	23	0	0	23	9	14	39.17	96.58
Germantown (16)[a]	New Brunswick, Canada	11	0	0	11	11	0	45.68	64.80
Great Falls (17)	Montana, USA	2	16	0	18	3	15	47.41	111.37
Great Swamp (18)	Rhode Island, USA	19	0	0	19	5	14	41.50	71.62
Gros Morne Nat. Park (19)[a]	Newfoundland, Canada	31	0	0	31	31	0	49.69	57.74
Haldimand (20)	Ontario, Canada	5	0	0	5	0	5	42.81	79.96
Holiday Beach (21)	Ontario, Canada	1	0	0	1	0	1	42.10	83.12
ISBP Ocean County (22)	New Jersey, USA	3	0	0	3	3	0	39.93	74.08
Jasper (23)	Alberta, Canada	0	9	0	9	7	2	52.98	118.10
KLAM (24)	California, USA	0	5	0	5	0	5	41.99	121.74
Lake La Biche (25)	Alberta, Canada	5	13	0	18	13	5	54.83	112.05
Lake Mead (26)	Nevada, USA	0	0	6	6	6	0	36.02	114.69
Last Mountain (27)	Saskatchewan, Canada	21	9	0	30	29	1	51.08	105.23
Lucky Peak (28)	Idaho, USA	0	5	0	5	5	0	43.53	116.05
Mary's River (29)	Nevada, USA	0	7	0	7	3	4	41.05	115.28
Meanock (30)	Alberta, Canada	0	5	0	5	0	5	54.57	113.33
Modoc (31)	California, USA	0	8	0	8	3	5	41.46	120.52
Mono County (32)	California, USA	0	14	0	14	3	11	37.92	118.87
Moose Park (33)	Saskatchewan, Canada	19	13	0	32	16	16	49.81	102.42
Mount Baker (34)	Washington, USA	0	7	0	7	4	3	48.50	121.50

Appendix 2. Continued.

Sampling sites	State or province, Country	East	West	South	N_{total}	N_{seq}	N_{rsa}	Latitude (°N)	Longitude (°W)
Oak Harbor (35)	Ohio, USA	9	0	0	9	4	5	41.62	83.22
Ponca State Park (36)	Nebraska, USA	25	1	0	26	7	19	42.60	96.73
Powdermill NR (37)	Pennsylvania, USA	18	0	0	18	5	13	40.20	79.24
Queen's Biol. Station (38)[a]	Ontario, Canada	21	0	0	21	21	0	44.58	76.32
RFSL (39)	California, USA	0	3	0	3	0	3	41.77	124.05
Ruby Lake (40)	Nevada, USA	0	11	0	11	3	8	40.00	115.33
Sarc (41)	California, USA	0	8	0	8	3	5	40.54	121.52
South Oregon (42)	Oregon, USA	0	22	0	22	6	16	42.43	123.44
Stevensville (43)	Montana, USA	0	9	0	9	3	6	46.52	114.05
Suffolk County (44)	New York, USA	2	0	0	2	0	2	40.73	73.19
Tatlayoko (45)	British Columbia, Canada	0	2	0	2	2	0	51.55	125.42
Terra Nova Nat. Park (46)	Newfoundland, Canada	2	0	0	2	0	2	48.53	53.93
Trois-Rivières (47)[a]	Québec, Canada	29	0	0	29	29	0	46.35	72.55
Vermilion (48)	Michigan, USA	19	4	0	23	3	20	46.76	85.15
Vernal (49)	Utah, USA	0	11	1	12	7	5	40.11	109.65
Vicksburg (50)	Michigan, USA	4	0	0	4	3	1	42.12	85.53
Walden (51)	Colorado, USA	2	26	0	28	5	23	40.50	106.17
Washoe County (52)	Nevada, USA	0	2	0	2	2	0	40.75	119.63
Waubay (53)	South Dakota, USA	3	0	0	3	3	0	45.43	97.34
Wenatchee (54)	Washington, USA	0	13	0	13	3	10	47.42	120.31
Whitehorse (55)	Yukon, Canada	0	1	0	1	1	0	60.72	135.05
Yosemite (56)	California, USA	0	10	0	10	3	7	37.85	119.57
Fall stopovers (site ID)									
Albuquerque (1)	New Mexico, USA	0	20	0	20	0	20	35.08	106.65
Back Bay (2)	Virginia, USA	6	0	0	6	0	6	36.60	75.97
Beatty (3)	Nevada, USA	1	8	0	9	0	9	37.00	116.73
Bosque del Apache (4)	New Mexico, USA	2	47	0	49	23	26	34.06	106.89
Braddock Bay (5)	New York, USA	12	0	0	12	0	12	43.31	77.71
Curry County (6)	Oregon, USA	0	8	0	8	0	8	42.84	124.54
Deep Creek (7)	Wyoming, USA	1	16	0	17	0	17	42.72	109.01
Eau Claire (8)	Wisconsin, USA	2	8	0	10	0	10	44.81	91.50
El Paso County (9)	Colorado, USA	0	3	0	3	0	3	38.83	104.52
Fort Morgan (10)	Alabama, USA	37	3	0	40	0	40	30.23	88.02
Haldimand (11)	Ontario, USA	22	0	0	22	0	22	42.81	79.96
Holiday Beach (12)	Ontario, USA	9	1	0	10	0	10	42.10	83.12
Jekyll (13)	Georgia, USA	21	0	0	21	0	21	31.07	81.41
La Moure County (14)	North Dakota, USA	1	11	0	12	0	12	48.84	97.87

Appendix 2. Continued.

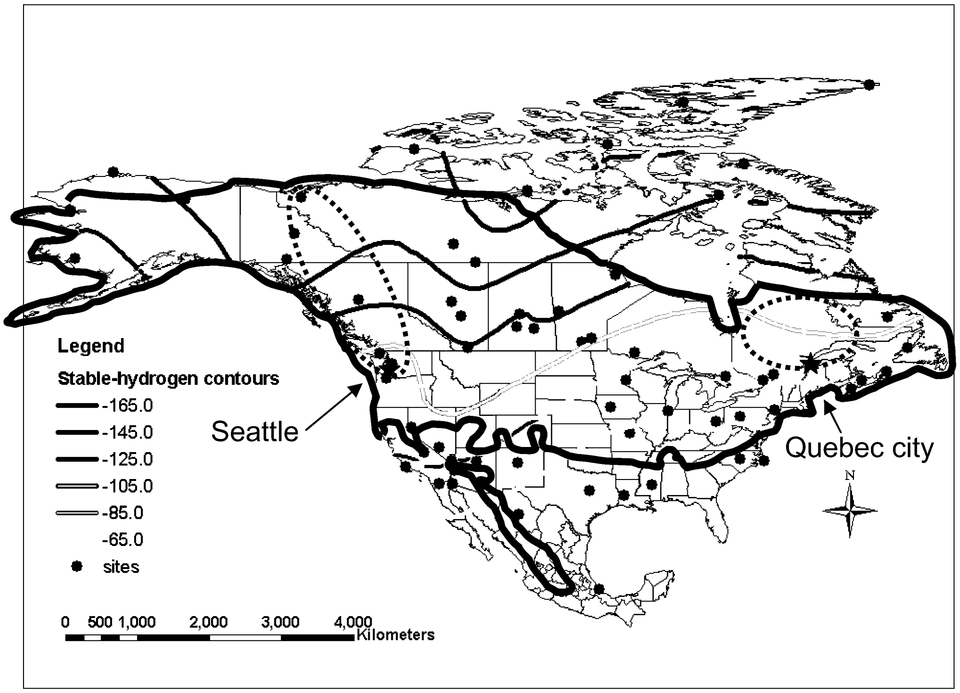
Sampling sites	State or province, Country	East	West	South	N_{total}	N_{seq}	N_{rsa}	Latitude (°N)	Longitude (°W)
Los Tuxtlas (15)	Veracruz, Mexico	2	6	0	8	0	8	18.50	95.17
Lucky Peak (16)	Idaho, USA	0	10	0	10	0	10	43.53	116.05
Modoc (17)	California, USA	0	25	0	25	0	25	41.46	120.52
Othon P. Blanco (18)	Quintana Roo, Mexico	2	1	0	3	0	3	18.50	88.30
Powdermill NR (19)	Pennsylvania, USA	11	0	0	11	0	11	40.20	79.24
Reserva Biosphera (20)	Tabasco, Mexico	0	3	0	3	0	3	18.52	92.73
Ruby Lake (21)	Nevada, USA	0	15	0	15	0	15	40.00	115.33
South Oregon (22)	Oregon, USA	0	12	0	12	0	12	42.43	123.44
Stanislaus County (23)	California, USA	0	10	0	10	0	10	37.55	121.00
Stevensville (24)	Montana, USA	0	15	0	15	0	15	46.52	114.05
Tehama and Glenn counties (25)	California, USA	0	26	0	26	0	26	40.03	122.12
Thunder Cape (26)	Ontario, Canada	2	0	0	2	0	2	48.30	88.93
Ulm (27)	Montana, USA	0	4	0	4	0	4	47.42	111.49
Vermillion (28)	South Dakota, USA	6	15	0	21	0	21	42.82	96.83
Wenatchee (29)	Washington, USA	0	3	0	3	0	3	47.42	120.31
Westport (30)	Minnesota, USA	0	21	0	21	0	21	45.72	95.17
Wintering sites (site ID)									
Baja California (1)	Baja California, Mexico	0	2	0	2	2	0	23.05	109.68
Belize (2)	Belize	0	1	0	1	1	0	17.53	89.10
Central Guerrero (3)	Guerrero, Mexico	0	1	0	1	1	0	18.52	99.58
Central Michoacan (4)	Michoacan Mexico	0	0	3	3	3	0	19.70	101.11
Central Oaxaca (5)	Oaxaca, Mexico	1	3	1	5	5	0	17.08	96.75
Chiapas (6)	Chiapas, Mexico	0	2	0	2	2	0	15.43	92.90
Colima (7)	Colima, Mexico	0	1	0	1	1	0	19.05	104.33
Jalisco (8)	Jalisco, Mexico	0	13	1	14	14	0	19.53	105.08
Los Tuxtlas (9)	Veracruz, Mexico	0	19	0	19	19	0	18.50	95.17
Michoacan coast (10)	Michoacan, Mexico	0	19	0	19	19	0	18.70	103.73
North Guerrero (11)	Guerrero, Mexico	0	6	0	6	6	0	17.98	102.15
Nuevo Becal (12)	Campeche, Mexico	0	2	0	2	2	0	18.33	89.33
Oaxaca coast (13)	Oaxaca, Mexico	0	4	0	4	4	0	15.95	96.65
Panama (14)	Canal zone, Panama	5	3	0	8	7	1	9.12	79.70
Poblano (–)	Campeche, Mexico	0	1	0	1	1	0	unknown	unknown
Puebla (15)	Puebla, Mexico	0	1	0	1	0	1	18.60	98.47
Quintana Roo (16)	Quintana Roo, Mexico	1	0	0	1	1	0	19.58	87.75
Sinaloa (17)	Sinaloa, Mexico	0	1	0	1	1	0	23.28	106.06
South Guerrero (18)	Guerrero, Mexico	0	3	0	3	1	2	16.85	99.92
South Oaxaca (19)	Oaxaca, Mexico	0	1	0	1	1	0	16.33	94.20

Appendix 2. Continued.

Sampling sites	State or province, Country	East	West	South	N_{total}	N_{seq}	N_{rsa}	Latitude (°N)	Longitude (°W)
Tabasco (20)	Tabasco, Mexico	0	10	0	10	10	0	17.98	92.916
Venezuela (21)	Venezuela	23	0	0	23	23	0	8.58	71.77
Yucatan (22)	Yucatan, Mexico	1	4	0	5	5	0	20.87	90.40
Spring stopovers (site ID)									
Alamo (1)	Nevada, USA	0	9	1	10	1	9	37.37	115.16
Back Bay (2)	Virginia, USA	17	0	0	17	0	17	36.60	75.97
Beatty (3)	Nevada, USA	0	36	2	38	3	35	37.00	116.73
Bosque del Apache (4)	New Mexico, USA	0	20	0	20	0	20	34.06	106.89
Braddock Bay (5)	New York, USA	40	1	0	41	0	41	43.31	77.71
Buenos Aires (6)	Arizona, USA	0	3	1	4	1	3	31.67	111.33
Collegeport (7)	Texas, USA	6	2	0	8	1	7	28.73	96.17
Douglas (8)	Arizona, USA	0	2	0	2	0	2	31.34	109.54
Driftwood (9)	Texas, USA	3	21	0	24	0	24	30.12	98.03
Eau Claire (10)	Wisconsin, USA	1	1	0	2	0	2	44.81	91.50
El Paso County (11)	Colorado, USA	0	1	0	1	0	1	38.83	104.52
Fishsprings NWR (12)	Utah, USA	0	20	0	20	0	20	40.22	112.74
Glenn County (13)	California, USA	0	1	0	1	0	1	39.60	122.43
Haldimand (14)	Ontario, Canada	15	0	0	15	0	15	42.81	79.96
Holiday Beach (15)	Ontario, Canada	4	0	0	4	0	4	42.10	83.12
IBSP Ocean County (16)	New Jersey, USA	20	0	0	20	0	20	39.93	74.08
Inyo County (17)	California, USA	1	20	21	21	1	20	36.58	117.42
Los Tuxtlas (18)	Veracruz, Mexico	2	10	0	12	0	12	18.50	95.17
Louisiana (Sabines NWR) (19)	Louisiana, USA	40	0	0	40	1	39	29.90	93.53
Michigan (20)	Michigan, USA	2	0	0	2	0	2	42.12	85.53
Modoc (21)	California, USA	0	1	0	1	0	1	41.46	120.52
Oak Harbor (22)	Ohio, USA	20	0	0	20	0	20	41.62	83.22
Powdermill NR (23)	Pennsylvania, USA	20	0	0	20	0	20	40.20	79.24
Reserva Biosphera (24)	Tabasco, Mexico	0	4	0	4	0	4	18.52	92.73
Sacramento (25)	California,USA	0	4	0	4	0	4	38.58	121.49
Salinas (26)	Veracruz, Mexico	15	25	0	40	0	40	18.92	95.97
South Oregon (27)	Oregon, USA	0	6	0	6	0	1	42.43	123.44
Suffolk County (28)	New York, USA	1	0	0	1	0	1	40.73	73.19
Vermillion (29)	South Dakota, USA	3	1	0	4	0	4	42.82	96.83
Vernal (30)	Utah, USA	0	5	0	5	0	5	40.11	109.65
Walden (31)	Colorado, USA	0	20	0	20	0	20	40.50	106.17
Waubay (32)	South Dakota, USA	10	2	0	12	0	12	45.43	97.34

[a] Sites included in Milot et al. (2000).

APPENDIX 3. Stable hydrogen contour map for feathers in North America.



Contours were obtained by kriging stable hydrogen ratios of weighted average growing-season values for precipitation in North America (Hobson and Wassenaar 1997, IAEA 2001) and by applying a correction factor of –25‰ to account for fractionation between rainfall and passerine feather fractionation (Wassenaar and Hobson 2001). The limits of the breeding range of the northern yellow warbler (Lowther et al. 1999) were added to illustrate that two sites (e.g., Quebec city and Seattle), though within the same isotopic region, may have a very different composition of breeding origins of migrants. Here, Seattle would receive migrants with a more extended range of values (i.e., from a wider array of isotopic regions) than Quebec city, because of the different latitudinal limits of the northern yellow warbler range in eastern and western North America.

Appendix 4. Statistical details of multicategory logit and logistic models describing spatial distribution of lineages. Sensitivity refers to the percentage of correctly predicted events (i.e., observing an eastern bird), whereas specificity refers to percentage of nonevents correctly predicted (i.e., observing a western bird). Abbreviations: E = east, W = west, S = south, n/a = option not available.

Seasons	Models	r^2	Deviance G^2 statistic	Pearson's χ^2 statistic	Deviance G^2 / df	Pearson's χ^2 / df	Sensitivity	Specificity
Breeding	Multilogit (E, W, S)	1.00	95.02 ($P = 0.72$)	193.28 ($P < 0.001$)	0.91	1.86	n/a	n/a
Winter	Logistic (E, W)	0.57	12.94 ($P = 0.28$)	22.15 (P = 0.28)	0.68	1.17	90.3%	96.9%
Spring	Logistic (E, W)	0.66	52.13 ($P = 0.003$)	244.67 ($P < 0.001$)	1.93	9.06	98.0%	96.0%
Fall	Logistic (E, W)	0.61	29.63 ($P = 0.20$)	73.77 ($P < 0.001$)	1.23	3.07	88.7%	98.6%

Breeding multicategory logit model: longitude: Wald $\chi^2 = 63.35$, df = 2, $P < 0.001$; latitude: Wald $\chi^2 = 45.29$, df = 2, $P < 0.001$, longitude*latitude interaction: Wald $\chi^2 = 49.40$, df = 2, $P < 0.001$.

Breeding logistic model: longitude: Wald $\chi^2 = 00.00$, df = 1, $P < 0.0001$.

Winter logistic model: longitude: Wald $\chi^2 = 28.68$, df = 1, $P < 0.0001$.

Spring logistic model: longitude: Wald $\chi^2 = 20.43$, df = 1, $P < 0.0001$.

Fall logistic model: longitude: Wald $\chi^2 = 89.57$, df = 1, $P < 0.0001$; latitude: Wald $\chi^2 = 13.43$, df = 1, $P = 0.000$.

Appendix 5

Kriging Models

We ran geostatistical analyses on the predicted probabilities obtained from multilogit models to illustrate gradual changes in the modeled global distribution of lineages and on precipitation data to build a continental δD map. We used ordinary kriging technique in the GEOSTATISTICAL ANALYST module of ARCGIS and followed the steps of the GEOSTATISTICAL WIZARD (Johnson et al. 2001). For each data set, we tested various options offered in GEOSTATISTICAL ANALYST: orders of trend removal to account for global spatial patterns, semivariogram models, anisotropy tool to account for directional influences, and search neighborhood methods (see Table 6 for list of selected models and their parameters). We verified models by examining cross-validation scatter plots, QQ plots, and diagnostic statistics. We selected models that had standardized mean prediction errors near zero, small root-mean-square prediction errors, average standard error near root-mean-square prediction errors, and standardized root-mean-square prediction errors near 1 (Johnson et al. 2001). In addition, we verified the quality of each kriging analysis by overlaying kriging contours with contours obtained from other interpolation methods and examining raw observed data and predicted values versus the value and location of the contours.

Table 6. List of models and parameters obtained from ordinary kriging analyses. Specific parameters of semivariogram models are indicated in the parentheses.

Data sets	Order of trend removal	Semivariogram model (Sill, minor axis, major axis, angle, nugget)
Breeding: east	Constant	Spherical (0.0017261, 41.80, 20.77, 349.7, 0)
Breeding: west	Constant	Spherical (0.0071877, 11.27, 11.27, 0.0, 0)
Breeding: south	Constant	Spherical (0.0059489, 16.66, 6.89, 84.9, 0)
Wintering	First	Hole effect (0.0.015438, 37.45, 15.07, 83.0, 0.00005007)
Fall	Second	Spherical (0.0064389, 33.59, 9.91, 30.0, 0)
Spring	First	Hole effect (0.025985, 25.19, 25.19, 0.0, 0)
δD in rain + 25‰ feather correction factor	First	Exponential (262.47,101.95, 52.84, 33.3, 49.653)