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Research Papers

Identification of Summer Origins of Songbirds Migrating through Southern Canada in Autumn

Détermination de l’aire estivale des oiseaux chanteurs qui migrent par le sud du Canada en automne

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ABSTRACT. Stable hydrogen isotopes (δD) in flight feathers were measured to investigate the summer origins of five species of boreal-breeding warblers captured during fall migration at Canadian Migration Monitoring Network (CMMN) stations spread across southern Canada. Mean δD varied among stations and species within stations, but there was broad overlap in δD values. Although isotope ratios indicate that migrants at each station come from a wide range of latitudes, they are unable to provide much longitudinal discrimination. Band recoveries are sparse, but indicate that in general western Canadian warblers move southeast in fall, eastern birds move southwest, and there is a transition zone in the Great Lakes region. Combining knowledge of migratory direction with isotope results increases discrimination of breeding areas. Isotope results support fall migratory movements by Blackpoll Warbler (*Dendroica striata*) and Northern Waterthrush (*Seiurus novaboracensis*) that are more easterly than for other species, and in all study species, birds from more northern regions passed through southern Canada later in the season. Migration monitoring stations capture birds from broad areas of latitude, and migrants passing through each province appear to come from largely different portions of the Canadian breeding range, so a few stations placed in each province should suffice collectively to sample birds from most of the boreal forest. Migration monitoring in southern Canada, therefore, has the potential to monitor status of boreal forest birds in Canada that are unsampled by other monitoring programs.

RÉSUMÉ. Nous avons mesuré les concentrations d’isotopes stables d’hydrogène (δD) dans les rémiges de cinq espèces de parulines qui se reproduisent dans la forêt boréale afin de déterminer l’emplacement de leur aire estivale. Ces parulines avaient été capturées pendant la migration automnale dans les stations du Réseau canadien de surveillance des migrations (RCSM) disséminées dans le sud du Canada. La valeur moyenne de δD variait selon les stations et selon les espèces capturées dans chaque station, mais il y avait un grand recoupement dans les valeurs de δD. Bien que les rapports isotopiques indiquent que les migrateurs de chaque station proviennent de latitudes très diverses, ils ne permettent pas une grande discrimination sur le plan longitudinal. Les bagues récupérées sont rares, mais elles indiquent qu’en général les parulines de l’Ouest canadien se déplacent vers le sud est en automne, que les oiseaux de l’est se dirigent vers le sud ouest et qu’il y a une zone de transition dans la région des Grands Lacs. En combinant les connaissances sur l’orientation de la migration et les résultats obtenus à l'aide des isotopes, on augmente la possibilité de distinguer les aires de reproduction. D’après les rapports isotopiques, la migration automnale de la Paruline rayée (*Dendroica striata*) et de la Paruline des ruisseaux (*Seiurus novaboracensis*) suivrait une trajectoire située nettement plus à l’est que celle des autres espèces et, chez toutes les espèces étudiées, les oiseaux provenant de régions plus nordiques traverseraient le sud du Canada plus tard dans la saison. Les oiseaux capturés aux stations de surveillance des migrations proviennent de latitudes très diverses et les migrateurs qui traversent chaque province semblent venir de portions très différentes de l’aire de reproduction au Canada. Par conséquent, quelques stations de surveillance réparties dans chaque province devraient suffire pour échantillonner les oiseaux de la majeure partie de la forêt boréale. La surveillance des migrations dans le sud du Canada pourrait donc permettre d’assurer le suivi des oiseaux de la forêt boréale du Canada qui ne sont pas échantillonnés dans le cadre d’autres programmes de surveillance.

Key Words: *breeding origin; deuterium; fall migration; stable isotopes*

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INTRODUCTION

The Canadian Migration Monitoring Network (CMMN), is a cooperative program of independent bird observatories spread across southern Canada (Fig. 1). A primary CMMN objective is to conduct standardized daily migration counts to monitor populations of northern-breeding migratory species, with a focus on passerines. The initial aim was to establish at least one migration monitoring station in each province so that individual species would be sampled from all parts of their ranges. However, because the breeding origin of migrants passing through a particular location is largely unknown, there is little basis for determining whether this goal has been met. Knowledge of breeding origin is also important for deciding whether migration counts from different stations can be pooled for analysis (Dunn 2005), and for determining where conservation action is needed when migration trends indicate it is warranted.

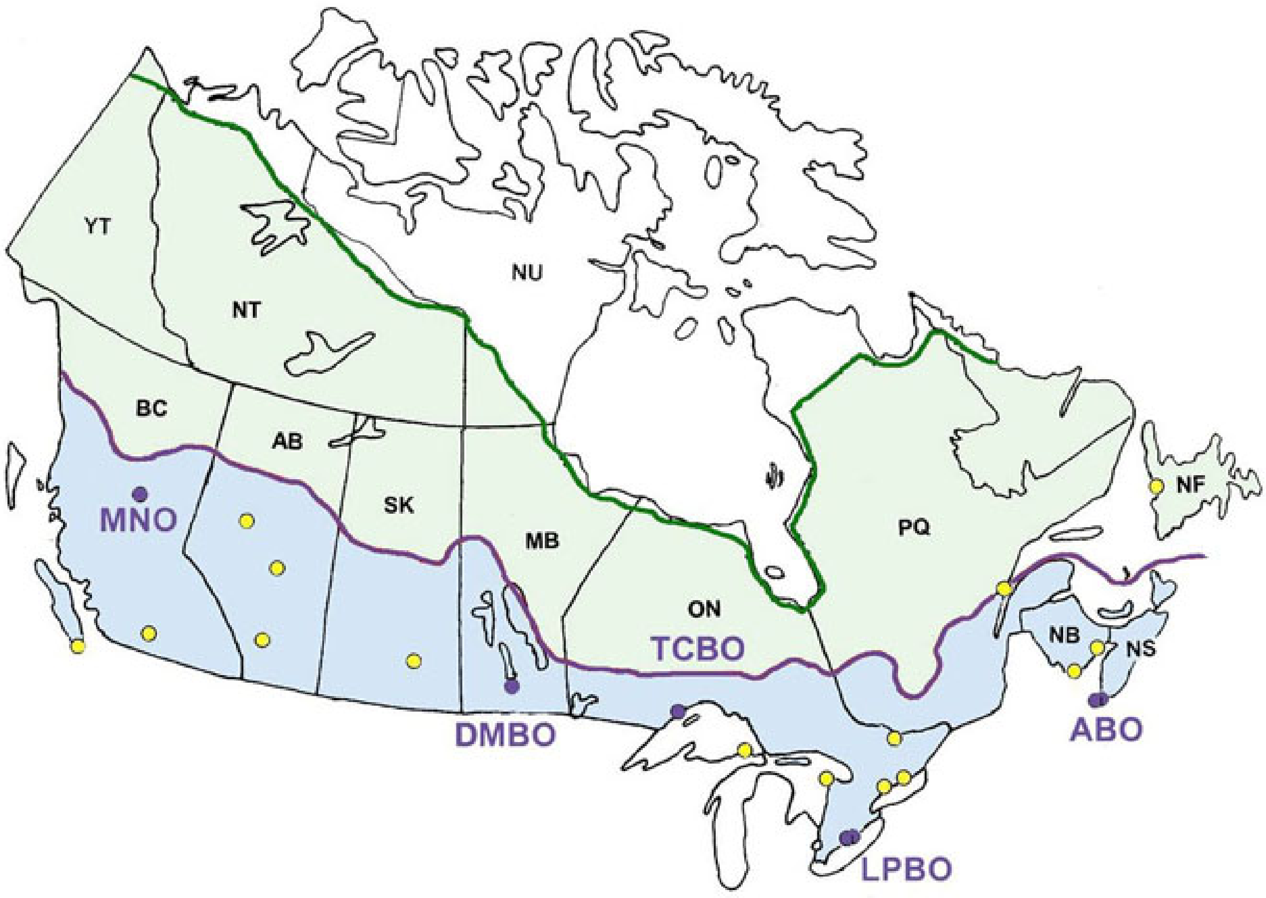
These questions would be of less importance if bird population status in boreal regions of Canada was monitored by other programs, but this is not the case. Species with less than two-thirds of their range sampled by the Breeding Bird Survey (BBS, http://www.mbr-pwrc.usgs.gov/bbs/bbs.html) are considered to be inadequately sampled for the purposes of documenting range-wide population trends (Bart et al. 2004). Over 40 Canadian-breeding passerines fall into this undersampled group (Rich et al. 2004), most of them boreal forest species with breeding range north of the limit of regular BBS coverage (Fig. 1). Many of them also winter south of the U. S., where they are not currently monitored. However, population trends can be derived from counts of birds during migration as they pass through populated parts of southern Canada and the U.S. Such trends have been demonstrated to be similar to BBS trends (Hussell et al. 1992, Pyle et al. 1994, Dunn et al. 1997, Ballard et al. 2003), especially when it is fairly certain that both surveys are sampling the same portion of the breeding range (Hussell 1997, Francis and Hussell 1998). Migration monitoring is, therefore, a high priority for Canada, and it is correspondingly important to learn the breeding origin of migrants at sampling stations.

Band recoveries of small birds are usually too few for identification of breeding areas, because of too low encounter frequencies of banded birds in general, compounded by the low probability of either banding or encounter within much of the boreal forest (Brewer et al. 2000). Nonetheless, across all species, a basic pattern of autumn migratory routes is discernible. Fall movements of insectivorous Neotropical migrants are, in general, southeast for western Canadian breeders and southwest for birds from the Maritime provinces, with a transition zone in Ontario through which migrants may move in those or intermediate directions (Brewer et al. 2000:10–11). Some species with populations in southern portions of western Canada (often subspecies that also breed in the western U.S.) have a more north–south migratory orientation, similar to the pattern shown by most western-breeding sparrows. Data from radar, which include all nocturnal migrants (not just passerines), depict similar patterns (Moore et al. 1995). Although these patterns provide broad clues as to the breeding origin of migrants passing through specific locations in southern Canada, the level of detail is insufficient to determine whether there is variation among species, or whether different migration monitoring stations sample overlapping or separate portions of the total population.

Analysis of stable hydrogen isotopes in feathers provides another tool for identifying the breeding origin of migrants. The ratio of deuterium to hydrogen (D:H, typically expressed as δD) in rainfall varies across North America in a fairly predictable, broad-scale geographic pattern (Fig. 2), and growing season rainfall values are reflected in local food webs (Cormie et al. 1994). That signal is translated through diet into the δD values of feathers grown by birds living in the area, both by juveniles growing their first set of feathers and by adults replacing molted feathers (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Stable-isotope signatures in passerine feathers have been used to determine latitudinal zones of natal or breeding origin in several species of birds (Wassenaar and Hobson 2000a, Hobson and Wassenaar 2001, Wassenaar and Hobson 2001, Meehan et al. 2001, Kelly et al. 2002, Rubenstein et al. 2002, Smith et al. 2003, Hobson et al. 2004).

Patterns of δD contours (Fig. 2) are approximate, not only because they are based on relatively few sample points, but also because isotopic signature is affected by altitude (Hobson et al. 2003, Meehan et al. 2004), and because patterns of δD in rainfall vary seasonally (International Atomic Energy Agency (IAEA) 2001) and annually such that zones can shift among years (IAEA 2001, Hobson et al.

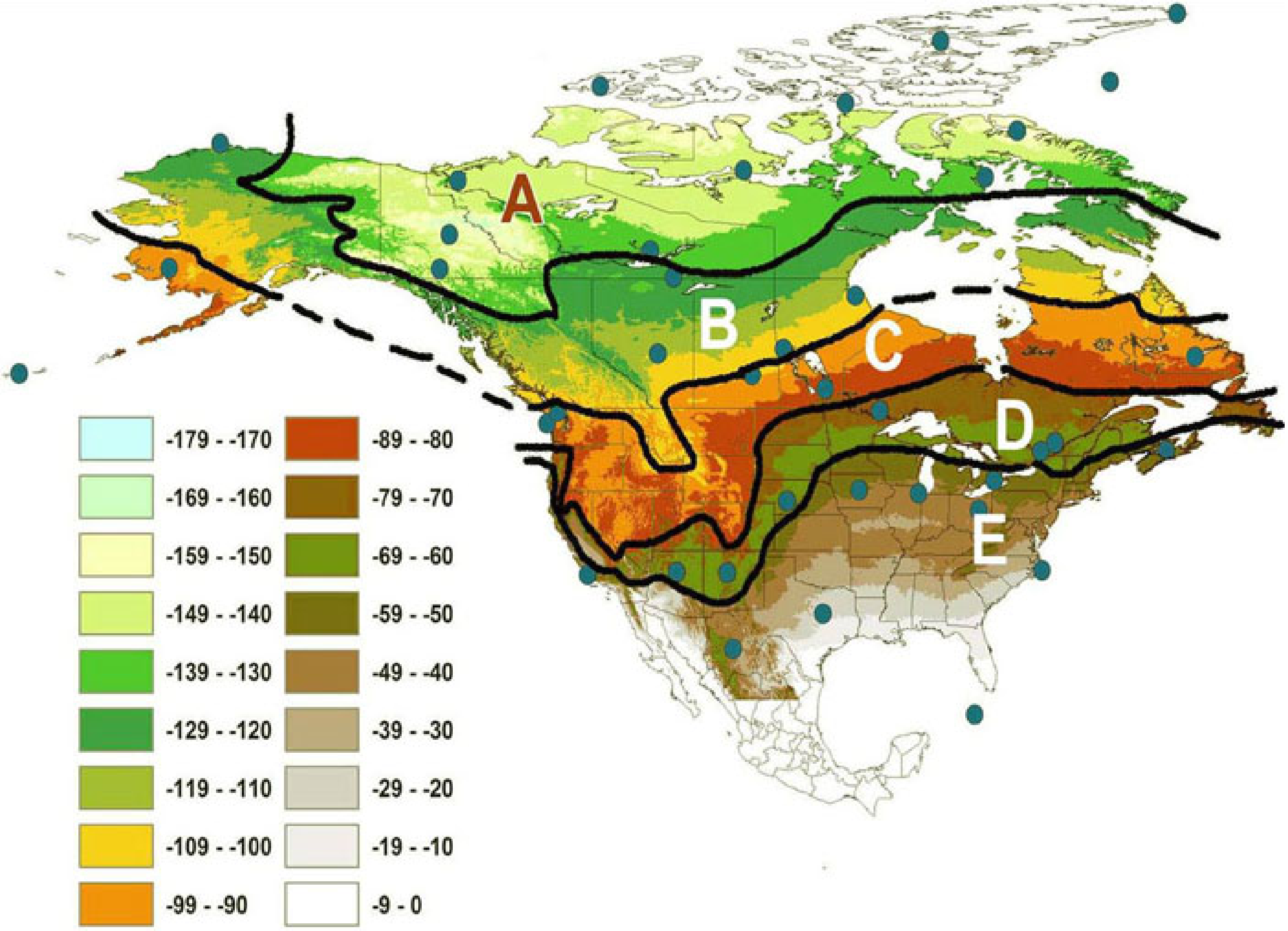
Fig. 1. Canadian Migration Monitoring Network (CMMN) stations (circles). Dark circles indicate stations contributing to this study (see text for full names). Pale shading shows the area of boreal forest that lies north of the region regularly sampled by the North American Breeding Bird Survey (dark shading). Abbreviations: DMBO = Delta Marsh Bird Observatory, LPBO = Long Point Bird Observatory, MNO = Mackenzie Nature Observatory, TCBO = Thunder Cape Bird Observatory, ABO = Atlantic Bird Observatory.



2003, Meehan et al. 2004, Bowen et al. 2005). Confidence intervals for average annual δD values of precipitation vary with location, ranging from about 2–8 parts per thousand (‰) in eastern Canada to about 7–13‰ for northwestern Canada (Online Isotopes in Precipitation Calculator http://www.waterisotopes.org/, Bowen et al. 2005), indicating the potential error in the location of the zone boundaries in Fig. 2.

There are also uncertainties in measurement of δD in bird feathers, which can vary 4–7‰ between individuals whose feathers grew at the same location (Hobson and Wassenaar 2001), and by a similar amount within individuals (Wassenaar and Hobson 2000b). Hobson et al. (2004) recently examined patterns of distributions of δD in feathers from breeding Ovenbirds (*Seiurus aurocapilla*) and

Fig. 2. δD (‰) in precipitation in North America during the growing season (after Meehan et al. 2004 and Bowen et al. 2005). Circles indicate precipitation stations where data were collected to build this map. Zones A–E were arbitrarily defined for purposes of this paper.



American Redstarts (*Setophaga ruticilla*) in central Saskatchewan. Although their study was designed to detect statistical outliers in order to identify individuals that may have dispersed into local breeding populations, their results suggest that ranges of the order of 12‰ might be reasonable to expect for single, philopatric populations. Finally, although δD in bird feathers is generally about 25‰ more negative than that in precipitation (Wassenaar and Hobson 2001) the relationship is not exact, and may vary geographically (Bowen et al. 2005, Hobson 2005).

Despite these sources of error, we believe that δD is appropriate for investigating broad geographic patterns in bird movements. Meehan et al. (2001) translated their error estimates for molt origins of Cooper's Hawks (*Accipiter cooperii*) into a latitudinal error of only about 1.5°.

Here we used δD measurements of feathers to investigate the breeding ground or natal origin of songbirds migrating through southern Canada. The method was expected to be less suited for longitudinal than for latitudinal discrimination of breeding areas, because of the orientation of δD contours (Fig. 2). Wassenaar and Hobson (2001), for example, found considerable overlap in δD values for Swainson's Thrush (*Catharus ustulatus*) captured at CMMN stations in two provinces (Delta Marsh Bird Observatory (DMBO) and Long Point Bird Observatory (LPBO), Fig. 1). However, we expected that combining stable isotope results with knowledge of general direction of migration, based on encounters of banded birds, would allow greater discrimination of breeding grounds than if either source of data were used alone.

METHODS

Feathers were collected during the 1998–2001 fall migration periods from five species that breed across Canada: Yellow-rumped Warbler (*Dendroica coronata*), Blackpoll Warbler (*D. striata*), American Redstart, Northern Waterthrush (*Seiurus novaboracensis*), and Wilson's Warbler (*Wilsonia pusilla*). Samples were collected at the five stations labeled in Fig. 1: Mackenzie Nature Observatory (MNO), DMBO, Thunder Cape Bird Observatory (TCBO), LPBO, and Atlantic Bird Observatory (ABO). The number of study sites and species was limited by the expense of analyzing samples, but stations contributing to the study sampled portions of the range where fall migrants were expected (from band encounters) to be moving south and southeast (MNO), southeast (DMBO, TCBO) and southwest (ABO). The fifth station (LPBO) was in the Great Lakes transition zone.

Birds were captured in mist nets or Heligoland traps during routine migration monitoring. Two tail feathers were collected (rectrix 4 from each side, chosen to minimize interference with flight capabilities, with the second sample saved for potential future analyses). Feathers were collected primarily from Hatch Year (HY) birds, because some adults of certain species are known to molt south of the breeding area. However, for all species included in this study, prebasic molt in After Hatch Year (AHY) birds is completed on the breeding grounds. About 10% of the feathers from LPBO, and <10% from TCBO, were collected from AHY birds. We were unable to detect any differences between age classes (unlike Smith and Dufty (2005)), and we retained the few AHY samples in the data set. Because our data were collected at different stations in different years, annual variation could not be separated from differences among stations. We were obliged to pool results from all years by site and species, and this may have added variability to our results.

All samples collected between 1 August and 31 October were included in analyses. Feathers were stored in paper envelopes, and later cleaned of surface oils using a 2:1 chloroform:methanol solution. Single tail feather subsamples (0.31–0.37 mg) were weighed into 4 x 6 mm silver capsules. Stable isotope analyses of the non-exchangeable hydrogen of feathers were conducted with continuous-flow isotope ratio mass spectrometry as described in detail by Wassenaar and Hobson (2003). Deuterium values are expressed in the delta notation, in units of parts per thousand, normalized on the VSMOW-SLAP standard scale. Origin of samples was assigned to geographic area according to the map in Fig. 2, assuming that feather δD is -25‰ (Wassenaar and Hobson 2001, Hobson 2005).

We used a general linear model (GLM) to investigate differences in mean δD among stations, and among species within stations. In no case did adjustment for effects of unequal sample sizes alter significance of results. The relationship between date and δD were examined with linear regression. Analyses were conducted using SAS/STAT v8.0, and all statistical tests report significance as $P < 0.05$.

RESULTS

Within each species, δD of feathers collected during fall migration generally became less negative from west to east (Fig. 3), in part reflecting the more northern location of western stations (Table 1). Pooled data for all species showed three groups of stations that had significantly different δD feather means: MNO and DBO in the west, TCBO and LPBO centrally, and ABO in the east (Table 1). These station groupings were often discernible for individual species, as well (Fig. 3). Nonetheless, within stations, isotopic signature varied significantly among species (Table 2). American Redstart had the most positive mean δD values at all stations (Table 2), corresponding to a more southerly origin, and Blackpoll Warbler usually had the most negative values (indicating a more northern origin).

We discuss results in detail by species and stations below.

Yellow-rumped Warbler

This species consists of two distinctive groups of races, Audubon's Warbler and Myrtle Warbler. We avoided collection of feathers from Audubon's Warblers, but MNO is within the zone of hybridization and inter-gradation between these groups, and some of the feather samples came from birds that could not be reliably assigned to race.

Yellow-rumped Warblers captured at MNO came 24% from zone B and 74% from zone A (Table 3). Origins from zone B northeast of MNO could not be ruled out by isotopic results alone (Fig. 4), but 90% of the birds at DMBO were from zones A and B, indicating a strongly southeastward fall movement by birds breeding northeast of MNO. Most migrants at MNO were, therefore, likely from the weakly differentiated race *Dendroica coronata hooveri*, which breeds in the northwestern portion of the range (Hunt and Flaspohler 1998), mainly northwest of MNO. TCBO had as many Myrtle Warblers from zones A and B combined (42%) as from zone C, also indicating primarily southeastward movement past that station (Fig. 4). Most Yellow-rumped Warblers at LPBO were from zones C and D (69%, Table 3), and could have come from any direction, but that station still picked up 28% of its Myrtle Warblers from the northwestern zones A and B (mostly from the latter). ABO was dominated by C- through E-zone birds (totalling 86% of the sample). Band encounters (Brewer et al. 2000) suggest most of these birds were likely to have been raised in northeastern Canada, but the small proportion of B-zone birds (14%) indicates that a few migrants can reach ABO from west of Hudson Bay. Nevertheless, the decreasing proportion of A-zone birds at TCBO and LPBO, and their absence from ABO, suggests that far northwestern breeders bypass Nova Scotia to the south.

Band recoveries were more abundant for Yellow-rumped Warbler than for other species in this study. Numerous records show movements between southern Canada (Alberta eastward) and the southeastern U.S. (as far west as Texas but mainly east of the Mississippi River; Brewer et al. 2000), in keeping with the scenario outlined above.

Blackpoll Warbler

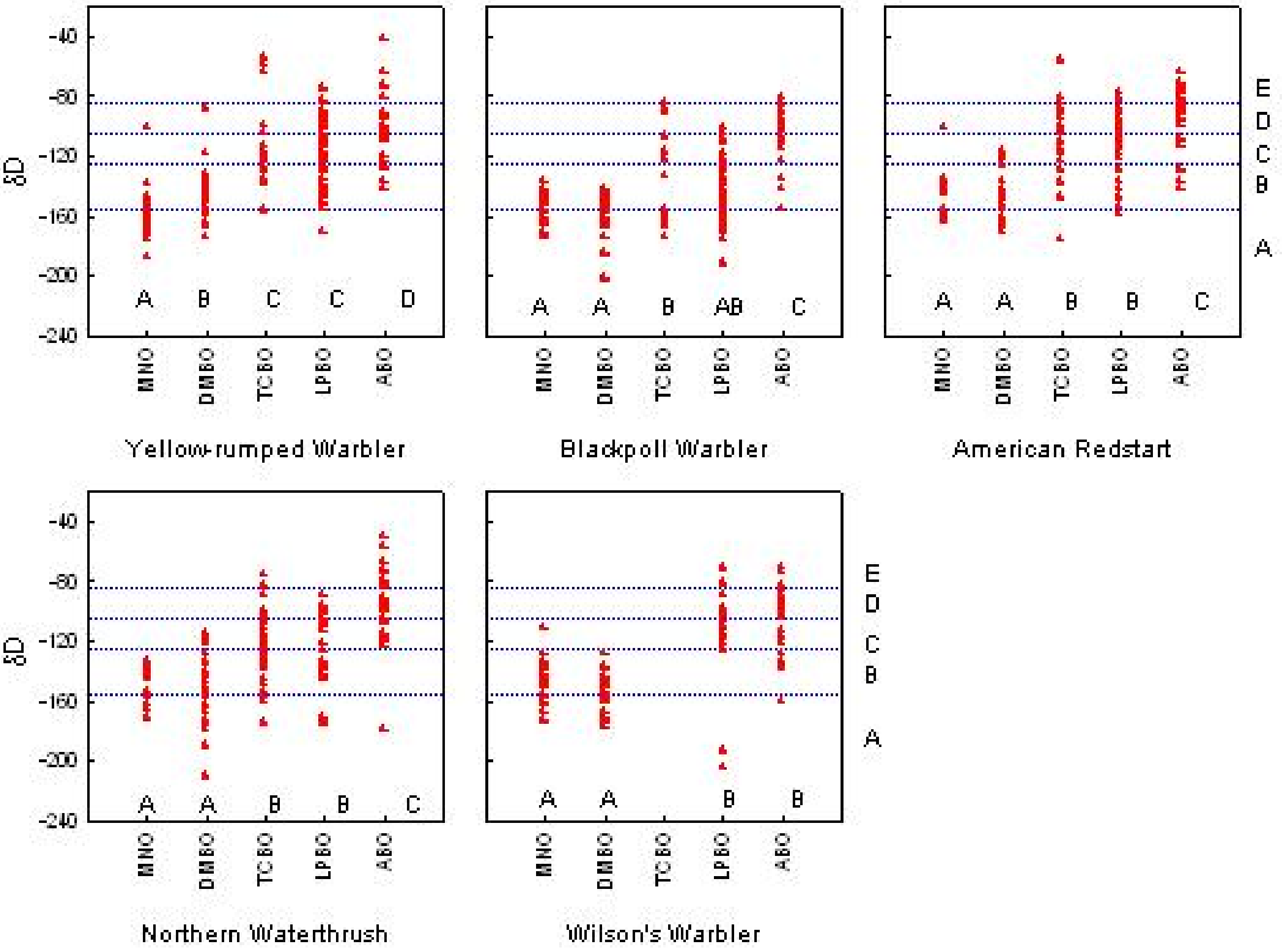
Sparse band recoveries for Blackpoll Warbler indicate that most birds move to the northern part of the U.S. Atlantic coast and depart over water from there, avoiding much of the southeastern U.S. (Hunt and Eliason 1999). Therefore, we would expect feather δD signatures to be dominated by birds from zones A and B at western migration monitoring stations, and should see relatively few D- and E-zone birds, except at ABO.

As expected, all Blackpoll Warblers found at MNO and DMBO were from zones A and B (Table 3), with many of the B-zone birds at MNO likely coming from Alaska (Fig. 5). Even at TCBO and LPBO, substantial numbers of Blackpolls (59% and 81%, respectively) were from the combined A and B zones. At ABO, isotope signatures from the C and D zones predominated (81%), indicating that large numbers of blackpolls at that station were raised in regions east of Hudson Bay and the Great Lakes. Although a few B-zone birds were also found (12%), indicating western origins, the relative scarcity of B-zone and absence of A-zone birds at ABO, combined with their presence at TCBO and LPBO, indicates that most Blackpoll Warblers raised in northwestern Canada and Alaska bypass ABO, reaching the Atlantic coast south of Nova Scotia.

American Redstart

The redstart's breeding range occupies very little of the feather δD A zone in the Yukon and Northwest Territories (Fig. 6), so we would expect to see relatively few A-zone birds at the study sites. Results generally agreed with this prediction (Table 3). The highest proportion of A-zone redstarts was at DMBO (24%, vs. only 10% at MNO), indicating southeastward movement. A- and B-zone birds together predominated at DMBO (72%), whereas the 28% of C-zone redstarts at DMBO suggest a fairly local origin (Fig. 6). At the two Ontario stations, C-zone redstarts were also strongly represented, and combined with the few A-zone birds at these sites, this indicates southeastward movement from Manitoba, northwestern Ontario, and even the Northwest Territories. D-zone redstarts predominated at both Ontario stations, suggesting additional contribution of migrants from more directly north (and possibly northeast) of these stations. Most ABO redstarts (57%) had E-zone signatures suggesting origins in eastern New

Fig. 3. Geographic pattern of feather δD by species, with stations arranged west to east. Grid lines (labeled on right-hand axis) indicate the arbitrarily defined δD zones shown in Fig. 2, but with values adjusted to reflect δD in bird feathers. Stations sharing the same letter along the x-axis did not differ significantly in mean feather δD (P < 0.05, Tukey-Kramer test for groups of unequal size).



Brunswick, Nova Scotia, and southern Newfoundland (Fig. 6, although reverse migration of a few individuals from New England is a possibility). Most other redstarts at ABO came from zone D, probably from the remainder of the Maritime provinces and Quebec. However, small numbers of redstarts at ABO from zones C and B indicate that a few western birds reach the Atlantic as far north as Nova Scotia.

Band recoveries for American Redstarts are sparse, but they clearly indicate that fall migratory direction shifts from southeastward for western birds to southwestward for eastern birds (Brewer et al. 2000), in conformity with the isotope results.

Northern Waterthrush

All Northern Waterthrushes at MNO were from zones A and B (Table 3), and those two zones also predominated at DMBO, with the addition of a few birds from the local zone C. MNO had more B- than A-zone waterthrushes, whereas DMBO showed the

Table 1. Geographic variation in feather δD values for five species of warblers (pooled) at CMMN stations, 1 August–31 October, 1998–2001. (Stations arranged west to east.)

Station	Latitude/longitude	Prov	δD zone[†]	Mean δD[‡]	Difference[§]	Sample size
MNO	55° 20’ N, 123° 10’ W	BC	B	-151	A	131
DMBO	50° 10’ N, 98° 10’ W	MB	C	-150	A	129
TCBO	48° 20’ N, 88° 50’ W	ON	D	-122	B	108
LPBO	42° 30’ N, 80° 10’ W	ON	E	-121	B	215
ABO	43° 20’ N, 66° 00’ W	NS	E	-96	C	150

[†] δD zone (Fig. 2) in which the station is located.
[‡] Adjusted means represent values if sample sizes were equal for all study species.
§ Means sharing the same letter did not differ significantly ($P < 0.05$).

reverse. This suggests that many waterthrushes at MNO were of local origin or came from central Alaska (zone B), whereas A-zone birds from eastern Alaska, the Yukon Territory, and Northwest Territories bypass MNO to the north and travel toward DMBO (Fig. 7). Zones A, B, and C combined were strongly represented in the migrants at TCBO (83%) and LPBO (78%), also indicating a strongly southeastward migration, but the A-zone proportions at these stations were lower than for Blackpoll Warbler. The C- and D-zone birds at LPBO (48% of the sample) could originate south, east, or west of Hudson Bay, but the relative scarcity of D-zone waterthrushes at LPBO (28%, compared with 49% in redstarts) suggests that many Ontario and western Quebec breeders move southeastward toward the Atlantic Coast, bypassing LPBO to the north. Some of these may reach the Atlantic Coast at ABO (among the 34% of D-zone birds there), but nearly half (46%) of the waterthrushes at ABO were from the eastern Maritimes E zone, and it is likely that a high proportion of the C- and D-zone birds also came from the Maritime provinces and Quebec. Consistent with this hypothesis, there was an almost total lack of A- and B-zone birds at ABO, suggesting that most Northern Waterthrushes from the far northwest reach the Atlantic coast south of Nova Scotia. A waterthrush banded at MNO 31 July 2003 was recaptured in North Carolina 17 September of the same autumn (V. Lambie, pers. comm.), supporting the strong easterly movement of western-breeding waterthrushes.

Wilson’s Warbler

Wilson’s Warblers at MNO were mainly from zone B (71% , Table 3), with 24% from zone A. That many of the B-zone birds were from Alaska is supported by a band recovery of a HY Wilson’s Warbler banded on the Alaska Peninsula on 14 August, 2000 and recaptured at MNO 27 days later (Eagan and Alder 2001). All birds sampled at MNO were likely from the northwestern race, *Wilsonia*

Table 2. Variation in feather δD values among species within locations for CMMN stations in southern Canada, 1 August–31 October, 1998–2001.

Station	Species	Mean δD	Significance of difference[†]	Sample size	Median date of data collection
MNO	American Redstart	-139	A	20	August 11
	Wilson’s Warbler	-144	AB	21	August 26
	Northern Waterthrush	-150	BC	19	August 22
	Blackpoll Warbler	-156	C	29	August 25
	Yellow-rumped Warbler	-158	C	42	September 9
DMBO	American Redstart	-141	A	29	September 1
	Yellow-rumped Warbler	-144	AB	28	September 13
	Wilson’s Warbler	-154	AB	22	August 23
	Northern Waterthrush	-155	AB	26	September 11
	Blackpoll Warbler	-157	B	24	September 11
TCBO	American Redstart	-110	A	26 (14)[‡]	August 23
	Yellow-rumped Warbler	-118	A	24 (15)[‡]	September 20
	Northern Waterthrush	-126	B	36 (26)[‡]	August 27
	Blackpoll Warbler	-136	B	22 (0)[‡]	—
LPBO	American Redstart	-106	A	51	September 1
	Wilson’s Warbler	-113	AB	19	September 8

(con'd)

	Yellow-rumped Warbler	-114	AB	64	October 6
	Northern Waterthrush	-126	B	23	August 25
	Blackpoll Warbler	-143	C	58	September 11
ABO	American Redstart	-86	A	39	August 31
	Northern Waterthrush	-91	AB	35	August 26
	Yellow-rumped Warbler	-100	AB	22	October 2
	Wilson’s Warbler	-102	B	28	September 3
	Blackpoll Warbler	-104	B	26	October 3

[†] Species are arranged within station by descending mean δD. Species sharing the same letter did not differ significantly in mean δD ($P < 0.05$, Tukey-Kramer test for groups of unequal size).

[‡] For TCBO, day of sample collection (used in a few analyses only) was lost for one year. Number of samples for which dates were known is shown in parentheses.

pusilla pileolata (Dunn and Garrett 1997; Fig. 8). Birds from zones A and B as defined in this paper also appear in the fall in New Mexico (Kelly et al. 2002), indicating a more north–south migration path for this subspecies than for the other birds in our study (see also Kimura et al. 2002, Clegg et al. 2003). Wilson’s Warblers at DMBO were evenly split between zones A and B, and probably consisted of the eastern race, *W. p. pusilla*, from eastern Northwest Territories and northern portions of the Prairie provinces. No Wilson’s Warblers were sampled at TCBO, but LPBO results showed a strong shift to zones C and D (combining for 68% of the sample), indicating that few of the Wilson’s Warblers sampled at LPBO originated west of Ontario (about the same proportion as for American Redstart, Table 3). The presence of E-zone birds at LPBO suggests that some individuals moving southwest from the Maritime provinces may reach the Great Lakes. The winter range of Wilson’s Warbler is primarily in Mexico and Central America, and the species is rare in Florida and the West Indies at any time (Ammon and Gilbert 1999). Therefore it is probably not normally a trans-Gulf migrant, and populations from the Great Lakes, as well as from northeastern North America, may migrate southwest in the fall. The majority of Wilson’s Warblers at ABO were from zone D, and, together with birds from the C zone, probably came from Quebec and the Maritime provinces. Nonetheless, a few individuals at ABO were from zones A and B, representing western origins.

Date Effects

Some of the variation in δD values can be explained by date on which feathers were collected. Within each station (all species combined), δD values became significantly more negative as the fall progressed (Fig. 9), indicating that individuals of more northerly origin were captured at later dates. In addition, regressions of δD on date for individual species within stations had negative slopes in 19 of 23 cases (statistically significant for nine). The only positive relationships (all non-significant) were for

Table 3. Distribution of feather δD values among isotopic zones (Fig. 2) by species, 1 August–31 October, 1998–2001.

Station	δD zone[†]	Species	A[‡]	B[‡]	C[‡]	D[‡]	E[‡]
MNO	B	Yellow-rumped Warbler	74	24	—	2	—
		Blackpoll Warbler	45	55	—	—	—
		American Redstart	10	85	—	5	—
		Northern Waterthrush	42	58	—	—	—
		Wilson’s Warbler	24	71	5	—	—
DMBO	C	Yellow-rumped Warbler	36	54	7	4	—
		Blackpoll Warbler	50	50	—	—	—
		American Redstart	24	48	28	—	—
		Northern Waterthrush	50	39	12	—	—
		Wilson’s Warbler	50	50	—	—	—
TCBO	D	Yellow-rumped Warbler	13	29	42	4	13
		Blackpoll Warbler	41	18	27	9	5
		American Redstart	4	19	31	35	12
		Northern Waterthrush	11	39	33	11	6
LPBO	E	Yellow-rumped Warbler	3	25	38	31	3
		Blackpoll Warbler	26	55	17	2	—

(con'd)

		American Redstart	2	12	31	49	6
		Northern Waterthrush	9	43	26	22	—
		Wilson’s Warbler	11	5	42	26	16
ABO	E	Yellow-rumped Warbler	—	14	27	36	23
		Blackpoll Warbler	—	12	27	54	8
		American Redstart	—	8	5	31	57
		Northern Waterthrush	3	—	17	34	46
		Wilson’s Warbler	4	11	14	54	18

[†] δD zone (Fig. 2) in which the station is located.
[‡] Percentage of δD values from this zone.

three species at MNO (American Redstart, for which there is little breeding range to the north of the station (Fig. 6); Blackpoll Warbler, and Wilson’s Warbler), and one at LPBO (Wilson’s Warbler). An ANOVA of the entire data set indicated that there were differences in slope of δD on date among species, although the amount of extra variation accounted for by species was relatively small (station: $F_{4,728}$=12.12, $P < 0.001$; species: $F_{4,728}$=1.51, $P = 0.20$; date: $F_{1,674}$=39.41, $P < 0.001$; stationXspecies interaction: $F_{14,709}$=7.04, $P < 0.001$; stationXdate interaction: $F_{4,675}$=0.42, $P = 0.80$; speciesXdate interaction: $F_{4,675}$=3.05, $P = 0.02$).

DISCUSSION

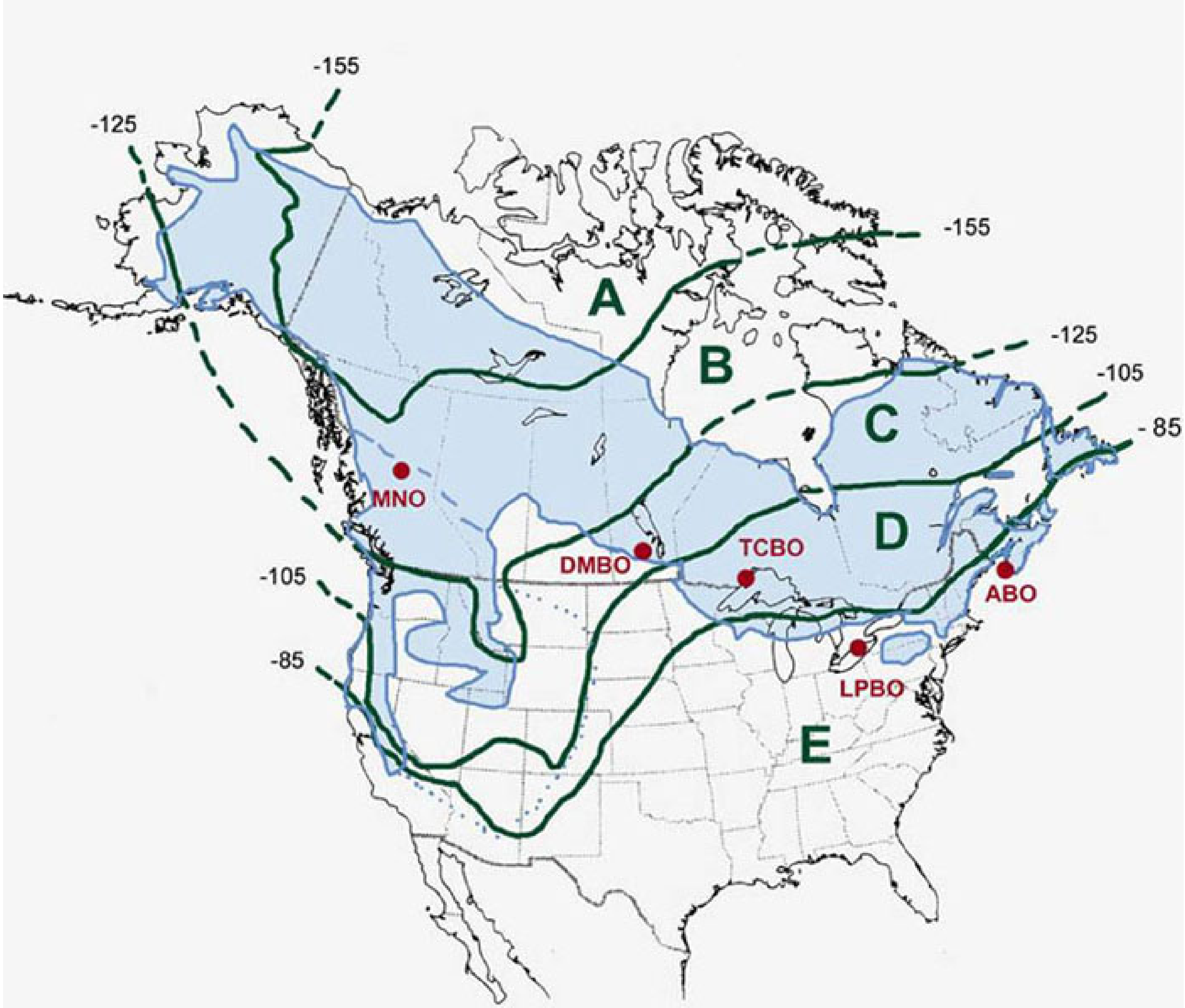
At each migration monitoring station, there was a broad range of feather δD values for every species, with birds originating from several isotopic zones (Fig. 3). The question of how broad a longitudinal range is sampled is more difficult to answer using hydrogen isotope data alone, because of the large degree of overlap in δD values among stations. Combining evidence from all sources, as in the species accounts above, allows us to draw some general conclusions about origin of migrants at each station.

The most westerly station (MNO), located in zone B, samples birds from Alaska, the Yukon and northern British Columbia. Possibly some migrants come from western Northwest Territories, as well. This station is located near a migratory divide between western races that migrate south through the western U.S. and boreal populations that move southeast toward the east coast (Kimura et al. 2002, Ruegg and Smith 2002), and appears to sample birds from both groups.

The DMBO station, in zone C, mostly samples birds from zones A and B that are moving to the southeast. DMBO migrants probably come primarily from the Yukon and Northwest Territories and the northern Prairie provinces, although some unknown proportion may originate from Alaska.

At TCBO, there is a high proportion of Blackpoll Warblers from zone A, in keeping with that species’ strong easterly movement, and high proportions of

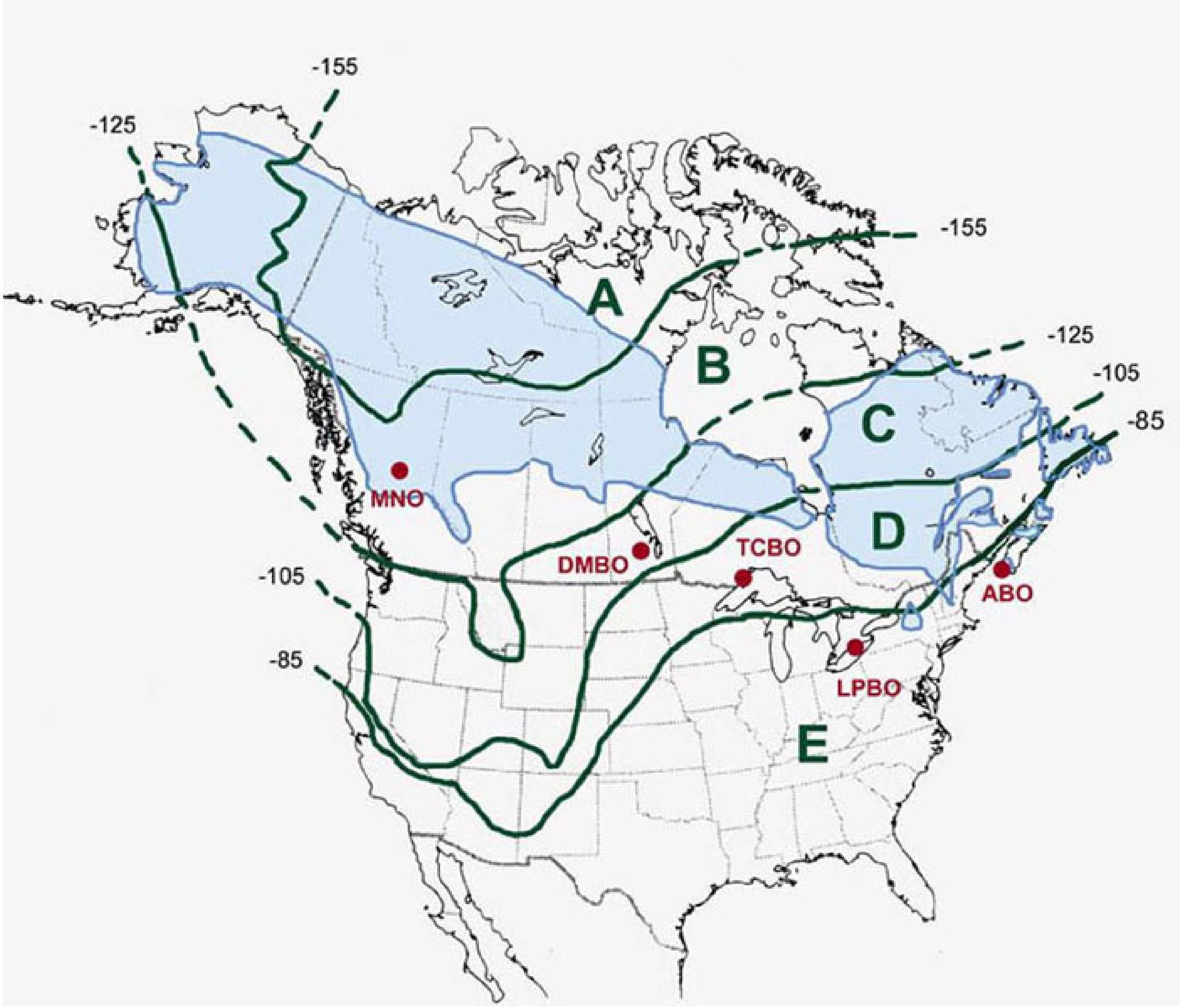
Fig. 4. Breeding range map for Yellow-rumped Warbler (after Dunn and Garrett 1997), with δD zones for feathers. The dashed blue line indicates the approximate boundary between "Myrtle" Warbler and "Audubon's" Warbler (which also breeds at scattered locations within the dotted blue line). Wintering area includes the southern half of the U.S. and most of Central America (Hunt and Flaspohler 1998).



other species from zones B and C, also to the northwest. Most of these birds probably come from northern Saskatchewan, Manitoba, and northwestern Ontario. However, TCBO also gets numerous birds from zone D, indicating movement more directly south from Ontario (especially in American Redstart). There is also a surprisingly high sprinkling of birds of all species from zone E (Table 3). The most likely explanation is that these are birds from the Maritime provinces headed southwest that took more westerly tracks than usual.

The LPBO station is more clearly in the transition zone of migratory directions, based both on isotopic

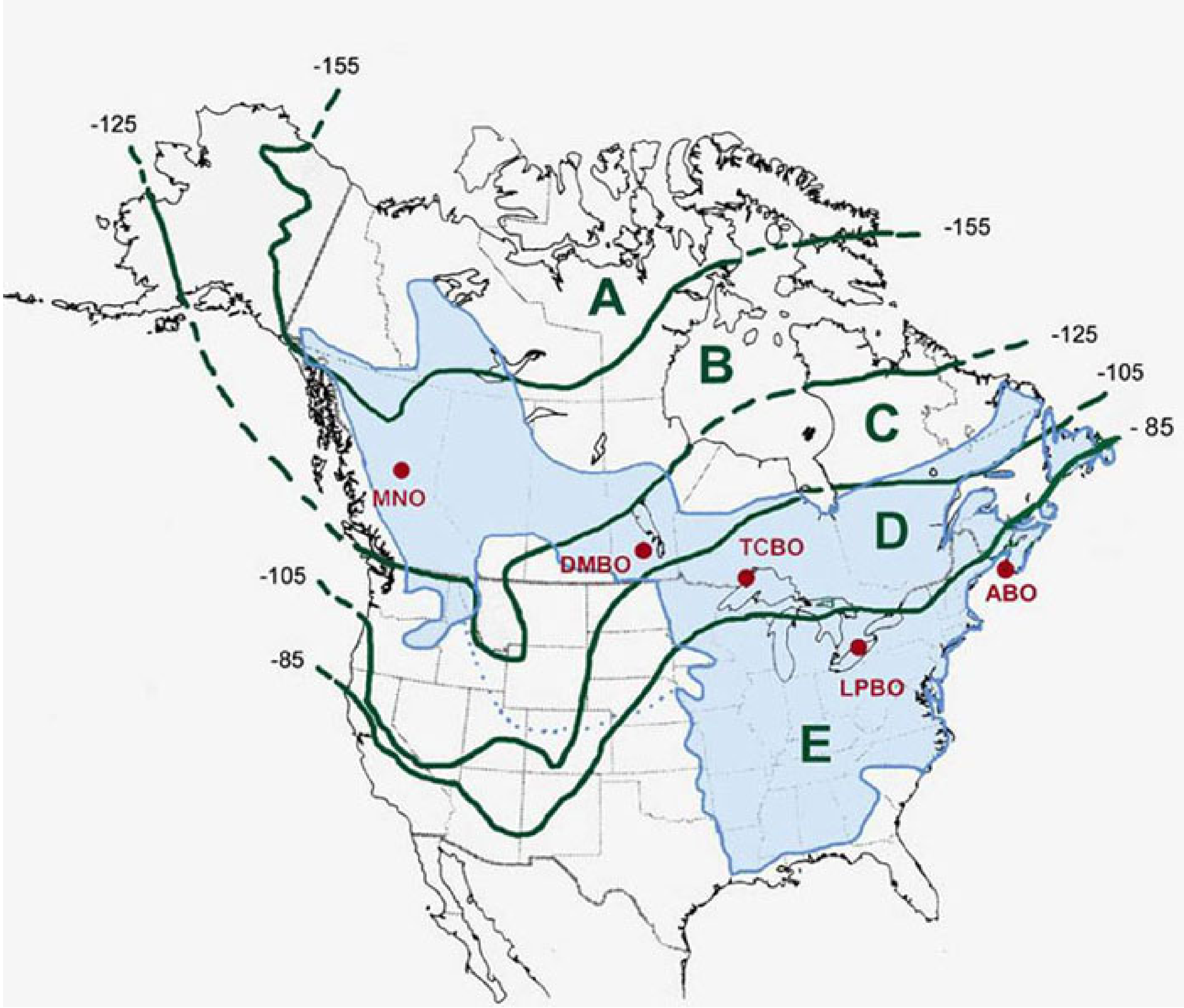
Fig. 5. Breeding range map for Blackpoll Warbler (after Dunn and Garrett 1997), with δD zones for feathers. Blackpolls winter in northern South America (Hunt and Eliason 1999).



evidence (Table 3) and band encounters (Brewer et al. 2000). Neither the isotope nor banding data clarify the proportion of fall migrants at LPBO coming from east of Ontario, although that proportion clearly varies among species. Blackpoll Warblers at this station are conspicuously from the west, whereas a substantial proportion of Wilson's Warblers come from the Maritime provinces (zone E). American Redstart is somewhere in the middle, with the highest proportion of individuals coming from zone D.

Finally, birds captured at ABO, in zone E, were primarily from zones D or E, depending on species (Table 3), in keeping with the numerous band recoveries of passerines moving southwest in fall along the Atlantic coast (Brewer et al. 2000). Small proportions of birds at ABO with isotopic signatures

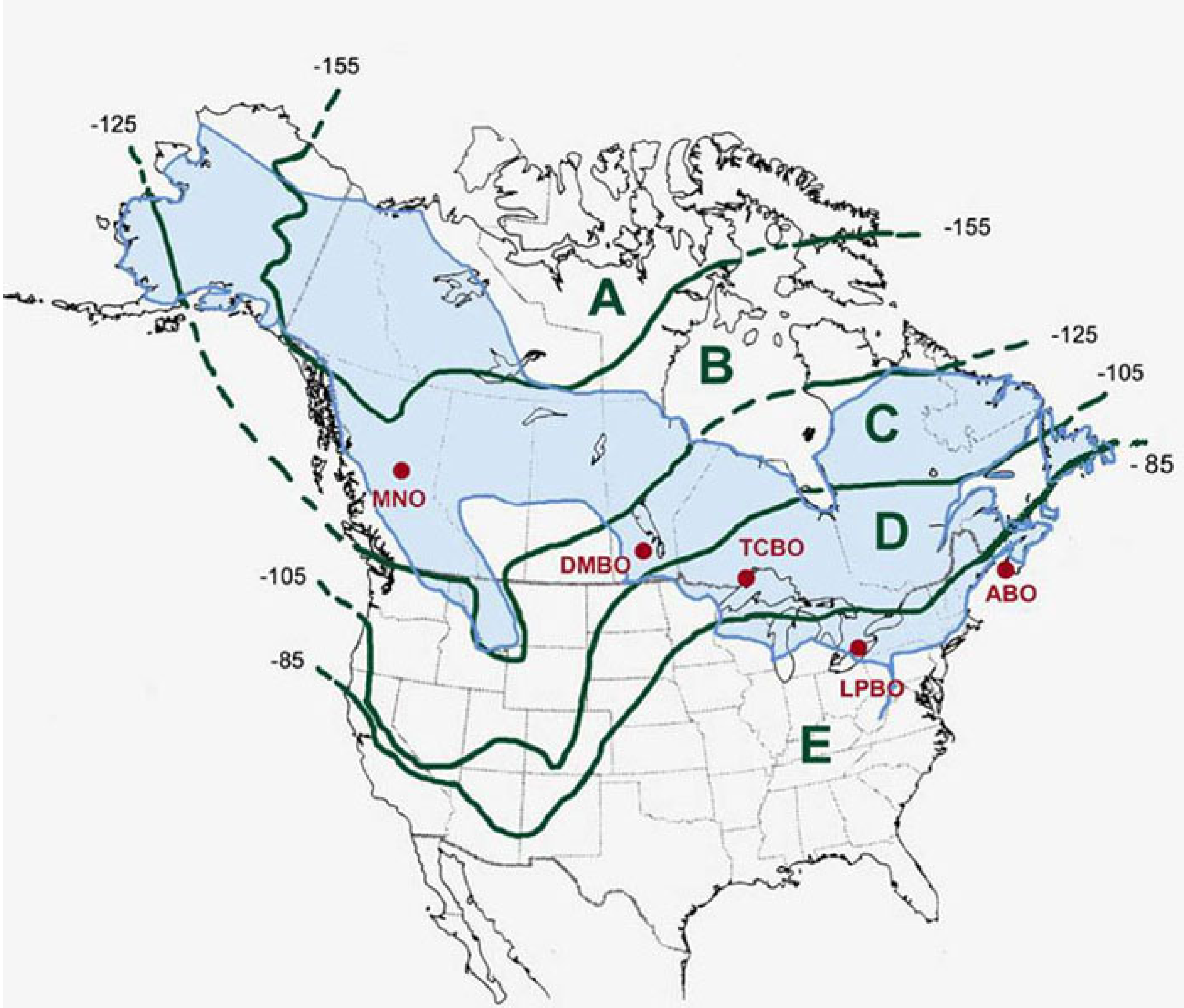
Fig. 6. Breeding range map for American Redstart (after Dunn and Garrett 1997), with δD zones for feathers. Redstarts also breed at scattered locations north of the dotted blue line. They winter primarily in the Caribbean islands, but also in Central America (mainly south of Mexico) and northern South America (Sherry and Holmes 1997).



of zones A and B indicate that a few birds of western origin do reach Nova Scotia, but most western birds reaching the Atlantic coast probably do so further south. Relatively high numbers of birds at ABO come from zone C, which might also be western (coming from eastern Manitoba or northwestern Ontario), but more likely originate from Quebec and Labrador. There are very few band recoveries connecting these areas to the Maritimes, but this could be an artefact of low human population density and low banding effort in those regions.

Our results suggest that CMMN's initial aim of establishing at least one station per province to

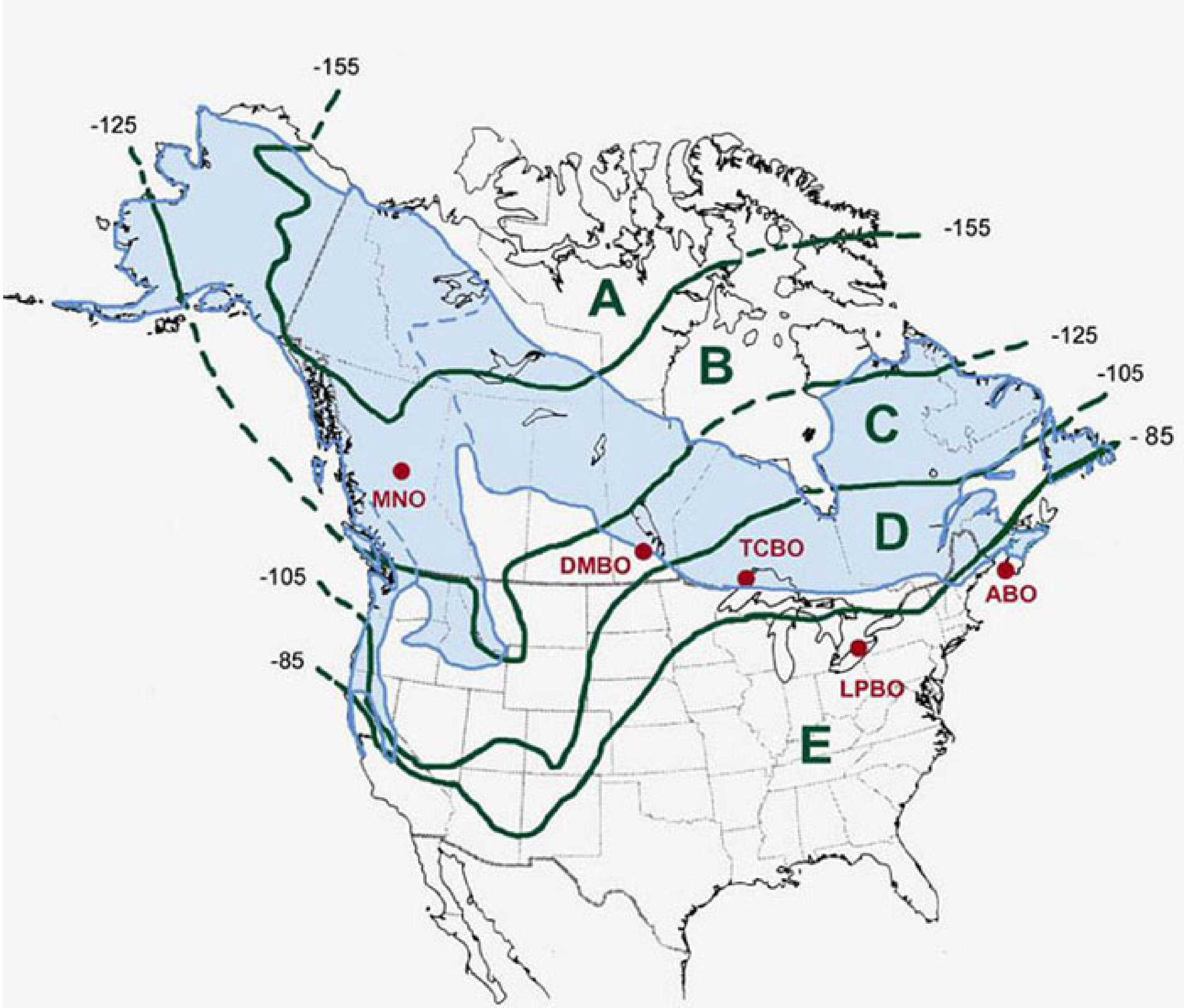
Fig. 7. Breeding range map for Northern Waterthrush (after Dunn and Garrett 1997), with δD zones for feathers. Winter range extends from southern Mexico and the Caribbean islands through northern South America (Eaton 1995).



sample birds across the entire Canadian breeding range was probably reasonable. Stations in adjacent provinces in this study appeared to sample largely different portions of the breeding range, but without large gaps in between. Ultimately, multiple stations should be established within each province to sample the same portion of the breeding range, to allow estimation of variance in population indices. As a starting point, we suggest that stations in southern Canada within about 400 km of one another (roughly 5° of longitude and latitude) are likely to be sampling the same portion of the breeding range, so their data could be pooled for combined analyses.

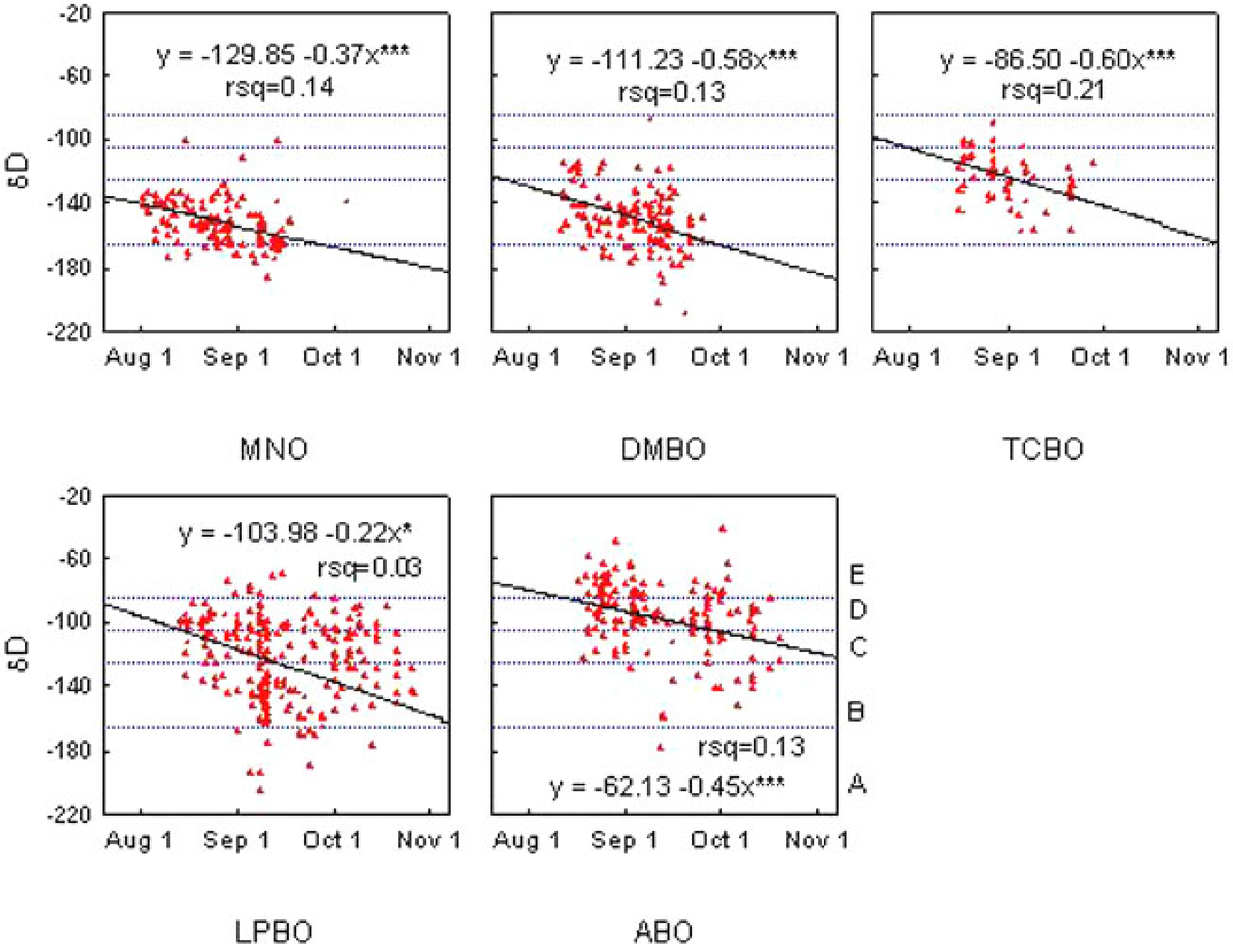
For species with breeding ranges confined primarily

Fig. 8. Breeding range map for Wilson's Warbler (after Dunn and Garrett 1997), with δD zones for feathers. Dashed blue lines indicate approximate boundaries of the races discussed in the text. Wintering area covers southern Mexico and much of Central America (Ammon and Gilbert 1999).



to Canada, some stations in the U.S. must be sampling the same populations as particular CMMN stations, and in theory could be used to monitor Canadian populations. However, the funnelling of fall migrants from western Canada into the eastern U.S. probably mixes migrants originating from very different portions of the Canadian breeding range, so population trends at U.S. stations may homogenize regional trends that are actually quite different. Similarly, it will be difficult to ascribe population trends at sites in the southern half of the U.S. to any particular portion of the Alaska-Canada breeding range. Migration monitoring close to the southern edge of a species' range will provide the most information on regional population trends.

Fig. 9. Feather δD values at each station as a function of date, all study species combined. Regression line significance: *** = P < 0.001, * = P < 0.05. Grid lines indicate the arbitrarily defined δD zones (labeled on right-hand axis) shown in Fig. 2, but with values adjusted to reflect δD in bird feathers.



Migration counts have long been assumed to involve birds coming from far to the north of sampling stations, and this study confirms that a single station indeed samples a very large area of latitude and longitude. This means that long-term trends in migration counts represent regional rather than local population change, such that range-wide population trends can be tracked with relatively few monitoring stations (perhaps several per province). A disadvantage of sampling a broad geographic area, however, is that migration trends do not allow identification of specific areas that might deserve conservation action. Our finding that birds of more northerly origin move through CMMN stations later in the season may help address this limitation. Potentially, data could be analyzed separately for each half of the season to determine whether population trends in more northern portions of each station’s catchment area differ from trends from more southern-breeding birds.

On average, warblers from the northern end of their range (with more negative feather δD values) pass through southern Canadian migration monitoring stations later than more southerly breeders, either because they begin migration later or simply take longer to reach southern Canada. One of the exceptions was Wilson's Warbler at MNO. Kelly et al. (2002) showed that Wilson's Warblers from high latitudes (including many from the A and Bs defined in this paper), passed through New Mexico earlier than birds that bred in the United States. Birds with northern feather δD signatures at both MNO and the New Mexico station were probably *Wilsonia pusilla pileolata*. Kelly et al. (2002) suggested a leapfrog migration pattern, in which Canadian and Alaskan Wilson's Warblers migrated earlier and moved farther south for the winter. The extent to which this pattern occurs in other species that have breeding range on both sides of the Canadian border has not been studied.

Analysis of δD documented different migration routes for different species, so study of additional species is warranted. We purposely selected species whose ranges extended across the continent, but study of species with more limited distributions (and limited range with particular δD zones) should prove illuminating. Also needed is research on feather δD values in spring migrants. In many species, both young-of-the-year and adults retain flight feathers grown at the natal or breeding area through the next breeding season. In spring, migration routes through the U.S. tend to follow a more north–south axis than in fall (Rappole et al. 1997, Hunt and Eliason 1999), with birds moving more directly to their breeding grounds. We would, therefore, expect fewer birds of western origin to pass through central and eastern Canadian stations in spring, and it may be easier to relate trends in spring migration counts to particular portions of the breeding range than is possible with fall migrants. Finally, geographic patterns may eventually be found in other stable isotopes or in genetic structure that could be used in combination with δD to define breeding grounds more precisely (Hobson 2005). To date, however, the useful variation found in other characters (such as C, N, S, and mtDNA) has not proved helpful for discriminating populations that breed in different parts of the interior portion of Canada's boreal forest zone (e.g., Kelly et al. 2005).

Feather δD values have limited utility for discriminating among Canadian breeding populations separated by longitude, because the δD zones are so broad. Banding data are too sparse by themselves to identify breeding grounds, but they provide convincing evidence of the overall direction of migration, allowing us to narrow the areas from which birds with particular isotopic signatures are likely to have come. Combining data from both sources allowed considerable insight into migration routes of individual species and probable catchment areas of migration monitoring stations across southern Canada. Results should prove useful in determining where new migration monitoring stations are needed, and in interpreting population trends from the Canadian Migration Monitoring Network.

Responses to this article can be read online at:
http://www.ace-eco.org/vol1/iss2/art4/responses/

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