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## STABLE ISOTOPE ANALYSIS OF FALL MIGRATION STOPOVER BY SIX PASSERINE SPECIES IN AN INLAND PITCH PINE-SCRUB OAK BARREN

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**ABSTRACT.**—We conducted mist-net surveys of migrating songbirds during fall migration 2007–2009 on the 1,300-ha Albany Pine Bush Preserve (APBP), a fire-managed inland pitch pine–scrub oak (*Pinus rigida*–*Quercus* spp.) barren in east-central New York. We banded 244 migrating passerines from 32 non-resident species in 8,610 net/m/hr documenting use of northeastern pine barrens as stopover sites for passerines with diverse breeding ecologies. We estimated the breeding site origin of six species (a kinglet, four warblers, and a sparrow) using stable hydrogen isotope measurements from flight feathers. There was a broad range of isotope ratios within each species indicating a large catchment area extending several hundred kilometers north and west of the stopover site. Over half the birds originated >750 km from the APBP. We found no evidence for geographical structure of the timing of migration through APBP; slopes of regression lines for capture date versus hydrogen isotope ratio from feathers ( $\delta D_f$ ) were not statistically different from zero. This contrasts with previous isotope research that reports both leapfrog and chain migration patterns by different warbler species at stopover sites in the western United States. Received 29 October 2010. Accepted 4 March 2011.

Pine (*Pinus* spp.) barrens are globally rare, pyrogenic, early-successional ecosystems that support unique assemblages of species including many rare and declining taxa (Finton 1998, Barnes 2003, Latham 2003, Wagner et al. 2003). Pine barrens in the northeastern United States are dry, nutrient-poor systems restricted to glacial outwash plains and ridges with shallow soils (Barnes 2003). Historically, these habitats were inhospitable to agriculture and remained undeveloped, but extensive suburbanization and suppression of wildland fire have reduced the region's pine barrens and other early-successional habitats >50% since the 1960s (Trani et al. 2001). There are <20 significant pine barrens remaining in the northeastern U.S. including three large, mostly contiguous coastal barrens and several smaller inland pine barrens (Fig. 1). Pine barrens transition to close-canopy forest in the absence of recurring fire (Finton 1998), but extant barrens appear to have persisted since glacial retreat 12,000–18,000 years ago (Barnes 2003) making them uniquely stable habitat for early-successional wildlife species.

Early-successional habitats in northeastern U.S. pine barrens are maintained almost exclusively through active management (Trani et al. 2001). The important targets of these efforts include

shrubland birds, the most conservation-reliant (*sensu* Scott et al. 2010) avian group in the region (Hunter et al. 2001, Dettmers 2003). Several studies have documented a 40+ year decline of shrubland and disturbance-dependent bird species (Brawn et al. 2001, Dettmers 2003), yet few published studies have described species–habitat relationships for birds breeding in northeastern pine barrens (Kerlinger and Doremus 1981a, b; Morimoto and Wasserman 1991; Grand et al. 2004; Beachy and Robinson 2008; Gifford et al. 2010). We know of no study that has documented the use of pine barrens as migratory stopover sites.

It is now well-recognized that events throughout the annual cycle are critical to survival of bird populations including factors in breeding and wintering areas, as well as at migratory stopover sites (Webster and Marra 2005). Migratory stopover sites are critical diurnal foraging areas for nearly all nocturnal migrants. Foraging resources and predation pressures differ among stopover habitats with important fitness consequences for migrants (Moore et al. 1995). Migrants select among alternative habitats and use stopover sites that maximize foraging efficiency (Moore and Aborn 2000). Most research on stopover sites has focused on woodland or riparian habitats (Winker et al. 1992, Wang et al. 1998), but some studies indicate that shrubland and forest interior breeding species rely disproportionately on early successional habitats during autumn migration (Rodewald and Brittingham 2004). Migratory connectivity of breeding and stopover sites has demographic, evolutionary, and conservation consequences

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FIG. 1. Significant pine barrens of the northeastern United States showing the location of the Albany Pine Bush Preserve.

(Runge and Marra 2005), and can be measured using stable hydrogen isotope ratios as intrinsic markers to trace movements of individuals (Wasenaar and Hobson 2001).

Stable isotopes of hydrogen are incorporated into avian tissues through diet in ratios that reflect a naturally occurring geographic gradient in rain water. Feathers, which are metabolically inert after they are fully replaced, hold an isotope ratio signature of the location where they were grown. Isotope ratios from feathers of migrating individuals that molt prior to autumn migration can be used to examine their approximate breeding latitude (Hobson 2002). These data can be used to estimate the catchment area of stopover sites (Mazerolle et al. 2005), and to connect populations passing through migration monitoring stations to breeding populations.

Our objectives were to: (1) describe the temporal dynamics and species composition of

the autumn migratory avifauna of the Albany Pine Bush Preserve (APBP), an inland pine barren in east-central New York, and (2) use stable hydrogen isotope measurements from feathers of captured birds to identify the breeding areas of selected migrant species using the APBP.

## METHODS

**Study Site.**—The 1,300-ha Albany Pine Bush Preserve is southwest of the confluence of the Mohawk and Hudson rivers in east-central New York State, USA ( $42^{\circ} 42' N$ ,  $73^{\circ} 52' W$ ) at an elevation of 79–110 m (Fig. 1). The Preserve supports at least 14 recognized terrestrial community types (Reschke 1990) but is dominated by a pitch pine (*Pinus rigida*)–scrub oak (*Quercus ilicifolia*, *Q. prinoides*) community (Schneider et al. 1991) with pitch pines in the overstory and scrub oaks and other shrubs (primarily Ericaceae) in the understory. Vegetation communities are

underlain by an extensive glacial outwash plain and a system of parabolic sand dunes (30 m max height) that is uniquely large and extensive compared to other northeastern pine barrens (Barnes 2003). Development, soil disturbance, and fire suppression between 1940 and 1990 resulted in an 81% change of land cover with 40% attributed to permanent habitat removal and 41% resulting from changes in plant community composition and structure (Finton 1998). Nearly half of the plant community change that occurred during this period (18% of total land cover) was replacement of pitch pine-scrub oak barrens and thickets with a closed-canopy deciduous forest, dominated by non-native, highly invasive black locust (*Robinia pseudoacacia*) (Finton 1998). The APBP is physically fragmented by a network of interstate and local highways, which create distinct blocks of protected lands adjacent to commercial, residential, and agricultural land uses. Ecosystem management, including prescribed fire, mowing, invasive plant removal, and restoration planting has been applied to >500 ha of the Preserve since 1991. The portion of the Preserve where we conducted our survey has supported a mosaic of open- and closed-canopy pitch pine-scrub oak communities since before 1928 (Finton 1998). The survey area contains the largest remaining block (56 ha) of pitch pine-scrub oak barrens in the APBP, encompassing several management units dominated by an open-canopy pitch pine overstory and a relatively dense mosaic of scrub oak and ericaceous shrubs in the understory. Sections of the sampled area experienced wild or prescribed fire in 1981, 1994, 1995, 1999, and 2005.

**Mist Netting.**—We deployed 6–8 mist nets (6–12 m long, 32–36 mm mesh) along a 0.5-km transect during fall migration 2007, 2008, and 2009. We began our survey in late August 2007 and continued until early November to insure that we sampled the full extent of the migratory period. We focused on the 6-week period from early-September to mid-October in subsequent years. Nets were placed on dune ridges perpendicular to the established foot path through the Preserve. Nets were opened at dawn (0530 hrs in early weeks, 0630 hrs in late weeks) and operated until 1030 hrs, 2–4 days per week. Nets were checked every half-hour and birds were removed to cloth bags for processing. Individuals of resident, non-migratory species (e.g., Downy Woodpecker [*Picoides pubescens*], Black-capped

Chickadee [*Poecile atricapillus*], Blue Jay [*Cyanocitta cristata*]), and of migratory species known to breed on the Preserve (e.g., Gray Catbird [*Dumetella carolinensis*], Eastern Bluebird [*Sialia sialis*]) were immediately released. Captured migrants were marked with a single aluminum USGS leg band, sampled for a single flight feather, measured, weighed, and released. We classified the age and sex of each bird when possible, but did not attempt to characterize the demographics of the fall migrant avifauna.

**Stable Isotope Analysis.**—We pulled a single flight feather (remex or rectrix) from each migrant and placed the feather in separate paper envelopes. We selected six species following our final field season on which to conduct hydrogen isotope analysis on the basis of sample size (> 5 individuals captured) and because they are known to completely molt all flight feathers on breeding areas prior to migration. These were Ruby-crowned Kinglet (*Regulus calendula*), Nashville Warbler (*Oreothlypis ruficapilla*), Magnolia Warbler (*Dendroica magnolia*), Palm Warbler (*D. palmarum*), Blackpoll Warbler (*D. striata*), and Lincoln's Sparrow (*Melospiza lincolni*). Information on molt schedules was obtained from individual Birds of North America species accounts (Ammon 1995, Williams 1996, Wilson 1996, Hunt and Eliason 1999, Swanson et al. 2008, Dunn and Hall 2010). These species have broad breeding ranges well north of our study site, extending across the boreal forest zone of the U.S. and Canada west to the Canadian Rockies (Nashville Warbler, Palm Warbler) or to Alaska (all other species). Two species (Magnolia Warbler, Nashville Warbler) have breeding ranges that extend into the temperate forest zone south of the study site.

We washed each feather to remove dirt and oils, first with a 0.1% Tween-20 detergent solution followed by two rinses in purified water. This was followed by two rounds of washing in a 2:1 chloroform:methanol solvent solution, each followed by rinsing in purified water. Cleaned feathers were placed in new paper envelopes and mailed to Colorado Plateau Stable Isotope Laboratory (CPSIL) at Northern Arizona University (Flagstaff) for weighing, encapsulation in tin, and hydrogen isotope-ratio mass spectrometry. The CPSIL uses a DELTA plus XL Thermo Electron gas isotope-ratio mass spectrometer to measure the hydrogen isotope ratio ( $\delta D_i$ ) from each feather sample. Machines and procedures are calibrated

so results are comparable to  $\delta D_f$  measured in other major research laboratories. Feathers were handled only with fine forceps during washing and subsequent processing.

A series of *t*-tests performed within each species indicated no significant differences in hydrogen isotope values from feathers collected in different years, and we pooled data from all 3 years in subsequent analyses. We regressed  $\delta D_f$  on capture date to examine possible trends with respect to timing of stopover of birds from different breeding localities. We converted  $\delta D_f$  to altitude-corrected growing-season precipitation values ( $\delta D_p$ ) using the equation  $\delta D_p = \delta D_f - 25\text{‰}$  (Mazerolle et al. 2005) and compared these to the growing season  $\delta D_p$  map for North America constructed by Meehan et al. (2004). We used ArcGIS (9.3.1) to overlay the  $\delta D_p$  map with digital maps of the breeding ranges for each species taken from Ridgely et al. (2007; downloaded from <http://www.natureserve.org/getData/birdMaps.jsp>). Area of origin maps were produced by highlighting the intersection of the breeding range with the observed range of  $\delta D_p$  values we calculated for each species.

RESULTS

We banded 244 migratory birds from 32 species in 8,610 net/m/hrs over 3 years (Fig. 2). Both number of migrants captured per unit effort and species diversity peaked in mid- to late-September, weeks 2 and 3 of our 6-week survey period (Fig. 2). Most species pass through the APBP in 2 or 3 weeks, but Nashville Warbler and Yellow-rumped Warbler (*Dendroica coronata*) are present over the course of 5 weeks. No species was captured in both the first and last week of the survey period. The fall migration begins with a trickle of warblers, quickly builds to a diverse assemblage of songbirds from several passeriform families, and ends with a large influx of cold-tolerant species, mostly sparrows that breed at very high latitudes and altitudes.

Stable hydrogen isotope values from feathers ( $\delta D_f$ ) of six species ranged widely, indicating the birds came from breeding sites across the boreal forest (Table 1). Mapped  $\delta D_p$  calculated from  $\delta D_f$  measurements overlapped with known breeding ranges of all species. Slopes of regressions between date of capture and  $\delta D_f$  were not statistically different from zero for all species (all  $r^2 < 0.05$ , all  $P > 0.05$ ). We found no correlations to indicate that individuals from more southerly breeding areas arrived earlier (chain migration) or that more

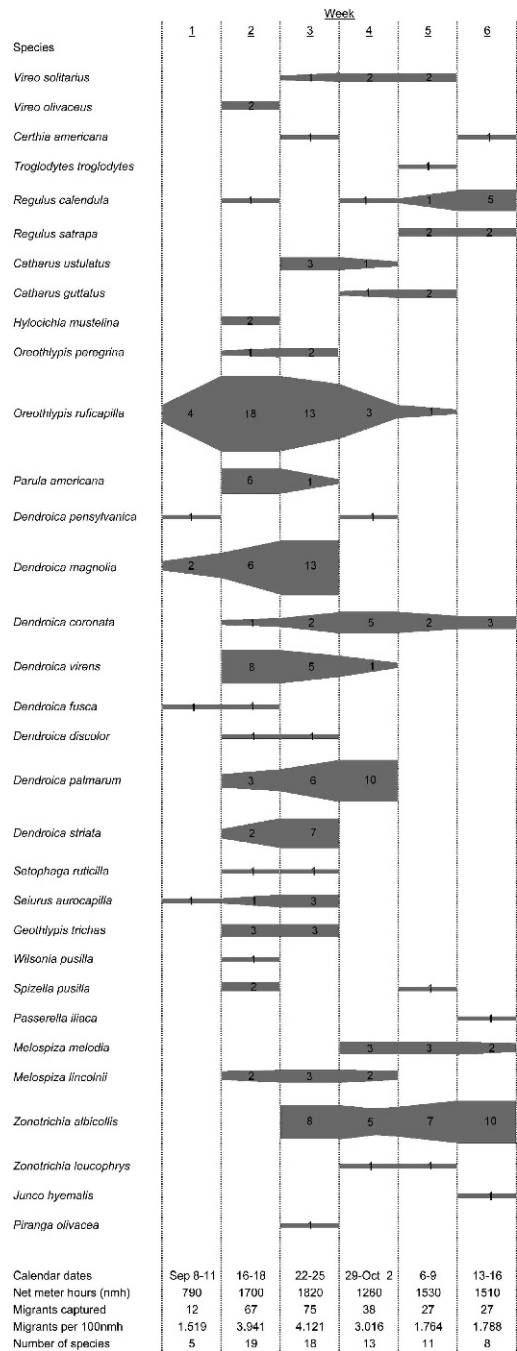


FIG. 2. Autumn migrants captured on the Albany Pine Bush Preserve during 6-week mist-net surveys in 2007, 2008, and 2009. Totals are for all 3 years combined.

TABLE 1. Stable hydrogen isotope values ( $\delta D_f$ ) from feathers of six species of migratory songbirds captured in the Albany Pine Bush Preserve in autumn 2007, 2008, and 2009.

Species	$\delta D_f$ Range	$\delta D_f$ Mean ( <i>n</i> )
Ruby-crowned Kinglet	-113.35 to -83.86	-109.14 (6)
Nashville Warbler	-118.69 to -82.93	-101.85 (13)
Magnolia Warbler	-116.78 to -80.15	-99.35 (8)
Palm Warbler	-123.75 to -68.10	-89.74 (19)
Blackpoll Warbler	-170.86 to -123.85	-148.64 (8)
Lincoln's Sparrow	-129.52 to -77.85	-97.34 (7)

northerly birds arrived earlier (leap-frog migration) (Fig. 3).

The generally east-to-west inclination of the isotope contours from the growing season model for North America precludes precise delineation of the longitude of the breeding sites of captured migrants. Our data indicate that 32 of 61 individuals from all six species had  $\delta D_f$  values  $< -100\%$ , corresponding to the  $-75\%$   $\delta D_p$  contour, which is at least 750 km north of the APBP (Fig. 4). Only for Palm Warbler (6 of 19 individuals) and Lincoln's Sparrow (2 of 7 individuals) did  $< 50\%$  of individuals originate southeast of the  $-75\%$   $\delta D_p$  contour. Blackpoll Warblers had  $\delta D_f$  values of  $-170.86$  to  $-123.85$  (mean of 8 measurements =  $-148.64$ ), indicating breeding sites that are at least 1,500 km north or northwest of APBP (Fig. 4). These patterns are noteworthy because all six species selected have

breeding populations in New York's Adirondack Mountains  $\sim 100$  km north of the APBP. It is possible that some Ruby-crowned Kinglets, Nashville Warblers, and Magnolia Warblers originated in the Adirondacks, but most individuals of even these species come from much farther north.

DISCUSSION

Our data indicate early successional habitat maintained by fire on inland pine barrens attracts migrating species that do not breed in these habitats. A number of the captured species breed in early successional shrubland habitats (e.g., Tennessee Warbler [*Oreothlypis peregrina*], Nashville Warbler), but most species captured breed exclusively in closed-canopy deciduous forests and spruce-fir (*Picea-Abies*) dominated boreal forests. We did not attempt to quantify the importance of pine barrens as stopover sites relative to other habitat types, but comparison of our capture data (Fig. 2) to those obtained over the same time period (Fall 2007–2009) at the well-studied Braddock Bay Bird Observatory (BBBO) indicates all species captured at APBP were also present at BBBO. The Braddock Bay site, on the southern shore of Lake Ontario near Rochester, New York,  $\sim 300$  km WNW of the APBP, supports a mosaic of abandoned fields, early-successional landcover, and second-growth forest (Bonter et al. 2007). A large staff of scientists and volunteers at BBBO operate 20–30 mist nets every day during the fall migration, resulting in a much greater effort

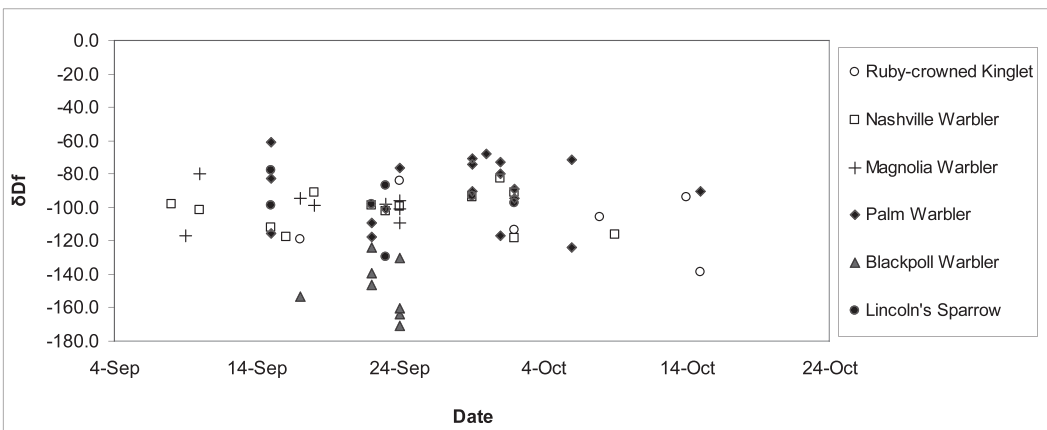


FIG. 3. Plot of stable hydrogen isotope values measured from feathers ( $\delta D_f$ ) of six species captured in the Albany Pine Bush Preserve and date of capture. Slopes of regression lines (not shown) are not statistically different from zero (Ruby-crowned Kinglet  $r^2 = 0.0487$ ,  $P = 0.67$ ,  $n = 6$ ; Nashville Warbler  $r^2 = 0.0084$ ,  $P = 0.75$ ,  $n = 13$ ; Palm Warbler  $r^2 = 0.0007$ ,  $P = 0.91$ ,  $n = 19$ ; Blackpoll Warbler  $r^2 = 0.0192$ ,  $P = 0.74$ ,  $n = 8$ ; Magnolia Warbler  $r^2 = 0.0096$ ,  $P = 0.81$ ,  $n = 8$ ; Lincoln's Sparrow  $r^2 = 0.0367$ ,  $P = 0.68$ ,  $n = 7$ ).

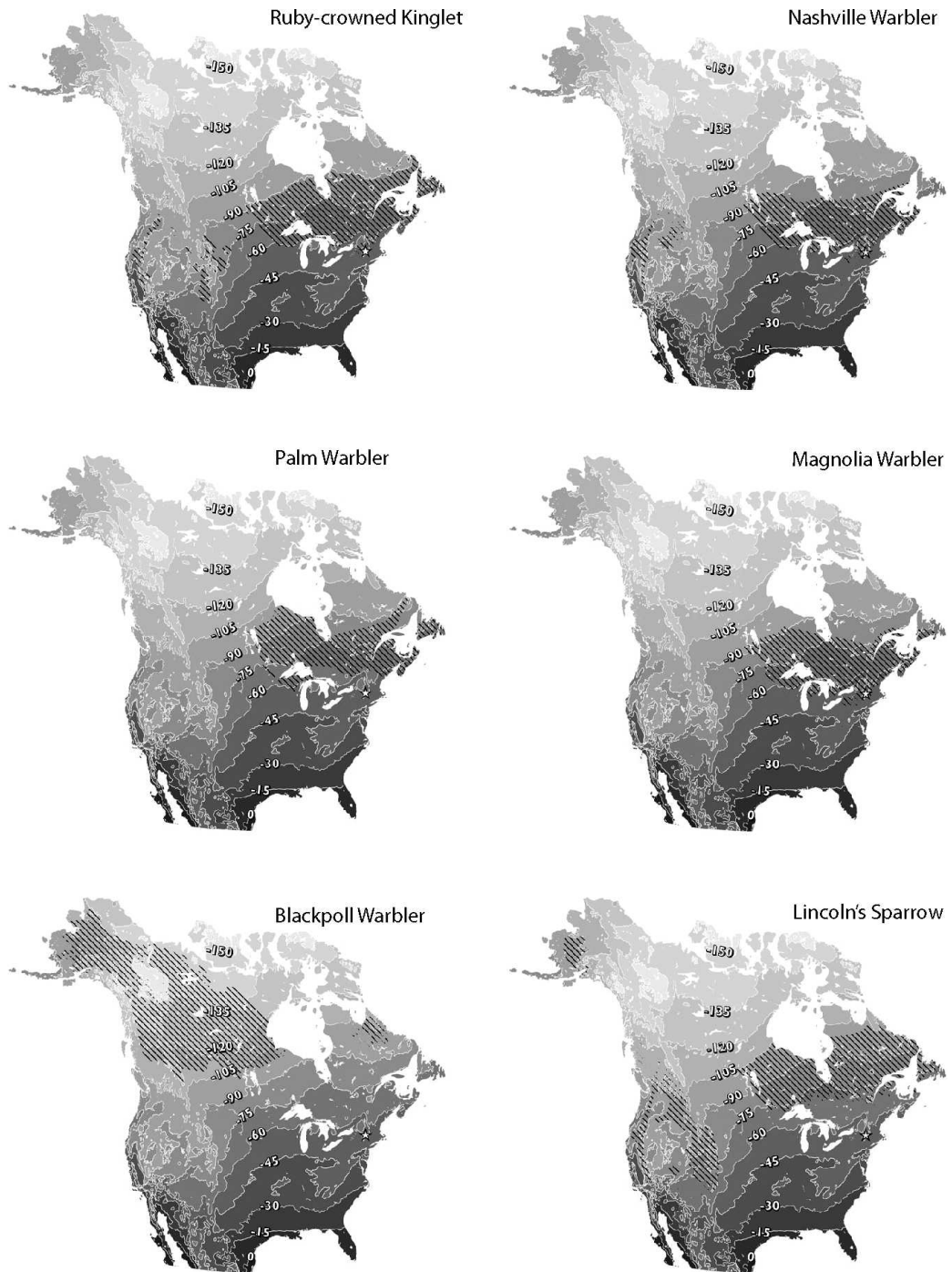


FIG. 4. Breeding range catchment areas for six passerine species captured in the Albany Pine Bush Preserve. Gray shading indicates the gradient of stable hydrogen isotope values in growing season precipitation ( $\delta D_p$ ) at 15‰ contours. Hatching indicates the overlap of the range of  $\delta D_p$  values obtained from feathers with the breeding range of each species. The star indicates the locality of APBP.

(net/m/hr) and higher observed migrant diversity. It is possible the APBP and other inland pine barrens are used as stopover sites simply because they have remained undeveloped islands of habitat in the expanding sea of suburban sprawl. Future research directed at addressing the relative importance of pine barrens as stopover sites should include controlled comparisons with similar size, nearby forests, agricultural landscapes, and riparian areas.

The list of species we captured surely underestimates the true diversity of autumn migrants that use the Albany Pine Bush Preserve as a stopover site. Species such as Wilson's Warbler (*Wilsonia pusilla*) and Fox Sparrow (*Passerella iliaca*) are represented by single captures, suggesting species diversity probably would increase if survey effort were greater. One of the primary limitations of mist netting as a survey tool is the bias toward capturing birds that forage mostly in the 2 m of vegetation closest to the ground (Remsen and Good 1996). This bias is probably less severe in the low-growing pitch pine–scrub oak habitat on the APBP than in forested habitats with higher strata available to feeding birds. Despite its limitations, our mist-net surveys expanded the list of bird species known to occur on the Albany Pine Bush Preserve (Barnes 2003, Gifford et al. 2010) and led to its designation in 2008 as a New York State Bird Conservation Area (McGowan and Corwin 2008).

Our hydrogen isotope analysis of the timing of stopover at the APBP with respect to latitude of breeding origin failed to reveal any correlation between stopover date and breeding latitude for our six target species (Fig. 3). Previous research (Kelly et al. 2002, Kelly 2006) has shown both negative and positive correlations for different fall migrating warbler species that stopover at the Bosque del Apache National Wildlife Refuge in New Mexico; some species (Orange-crowned Warbler [*Oreothlypis celata*], Common Yellowthroat [*Geothlypis trichas*]) breeding at southern latitudes arrived earlier than birds breeding at northern latitudes, whereas for other species (Yellow Warbler [*Dendroica petechia*], Wilson's Warbler) the reverse was true. Our failure to find any trends by our six study species may be due to our small sample size, although Kelly et al. (2002) had similar sample sizes of Common Yellowthroat ( $n = 19$ ), Orange-crowned warbler ( $n = 17$ ), and Yellow Warbler ( $n = 18$ ). Ours is the first attempt to use the hydrogen isotope approach to characterize the chronology of migration within

species in eastern North America, and our results indicate migration through eastern North America is less geographically structured than in the western U.S. Several other fundamental differences exist between the eastern and western songbird migration systems (Kelly and Hutto 2005) including taxonomic composition, relative use of fat metabolism, diet, and habitat use. Movement patterns are also apparently highly variable among passerine species (Kelly et al. 2002, Kelly 2006), and fall migration may be geographically structured in other species that pass through our study site.

The isotope data indicate catchment areas for all six study species were large and extended to regions of the boreal forest hundreds of kilometers from our study site (Fig. 4). This finding is similar to previously reported catchment areas estimated for other species of passerines at migration monitoring stations in Manitoba (Wassenaar and Hobson 2001, Mazerolle et al. 2005) and southern Ontario (Wassenaar and Hobson 2001). Thus, catchment areas of migratory stopover sites vary considerably among species. The estimated catchment areas of five of our six study species included regions north of the APBP, and extending well to the east and west (Fig. 4). The isotope approach does not allow distinguishing among all potential source areas within a given  $\delta D_p$  contour. Thus, it is not possible to identify how far east or west the birds that stopover on the APBP may originate. Most passerine species migrate in a generally north-south direction that parallels mountain ranges, major river valleys, and coastlines. We suspect the catchment areas we mapped overestimate the western extent of true catchment areas, and populations originating near the western edge of our catchment areas are not passing through APBP. An exception may be the Blackpoll Warbler, which has a unique trans-oceanic migratory pathway (Nisbet et al. 1995, Hunt and Eliason 2001). Individual Blackpoll Warblers migrate in a general eastward direction, collecting along the Atlantic Coast in Maritime Provinces and the northeastern United States. Blackpoll Warblers then migrate over the Atlantic Ocean to wintering areas in northern South America. Our data support the hypothesis that individuals breeding just north and east of the APBP in New York, New England, Ontario, and the Maritime Provinces do not pass through APBP as they migrate east.

Our hydrogen isotope analysis of six species



that pass through the APBP adds taxonomic and geographic breadth to research on the timing of songbird migration and quadruples the number of species for which catchment areas have been estimated with this method. Wassenaar and Hobson (2001) found the catchment area for Swainson's Thrushes (*Catharus ustulatus*) was much larger at Long Point, Ontario, than at Delta Marsh in Manitoba, suggesting that sites further along a migratory pathway will have larger catchment areas. The APBP may draw migrants from a larger area because it is southeast of those stopover sites. Comparisons among sites and among species may result in new insights regarding migratory pathways and the importance of specific stopover habitats as more hydrogen isotope data are published.

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