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Source: The Wilson Journal of Ornithology, 123(3):521-535. 2011.
Published By: The Wilson Ornithological Society
DOI: 10.1676/10-130.1
URL: http://www.bioone.org/doi/full/10.1676/10-130.1

The Wilson Journal of Ornithology 123(3):521–535, 2011

LARGE-SCALE MOVEMENT AND MIGRATION OF NORTHERN SAW-WHET OWLS IN EASTERN NORTH AMERICA

SEAN R. BECKETT[1] AND GLENN A. PROUDFOOT[1,2]

ABSTRACT.—We used information compiled by the U.S. Geological Survey's Bird Banding Laboratory and geographic information systems (GIS) analysis to identify trends in annual Northern Saw-whet Owl (*Aegolius acadicus*) movement across eastern North America. Analysis of 81,584 Northern Saw-whet Owl banding events revealed a southbound annual fall migration front with peak banding activity occurring progressively later in the season as latitude decreases. Northbound owls comprised <9% of owls banded and recaptured elsewhere in the same season, and <5% were recaptured northbound >100 km from banding location. There was no relationship between banding latitude and adult-to-juvenile ratio. However, the proportion of adults versus juveniles banded was not uniform among banding stations, suggesting age-differentiated migration patterns may exist. Information from multiyear foreign recaptures revealed that 72% of owls banded and subsequently recaptured at the same latitude in different years were recaptured <100 km from banding location. A similar trend was found in the Appalachian Mountains, the Great Lakes Basin, and the Atlantic seaboard. This indicates that Northern Saw-whet Owls may exhibit high migration route fidelity. These findings expand the Northern Saw-whet Owl information portfolio and illustrate the versatility of aggregate data sets as a tool for answering large-scale questions regarding migration. *Received 22 August 2010. Accepted 8 February 2011.*

The Northern Saw-whet Owl (*Aegolius acadicus*) is a common but poorly-understood member of the North American forest fauna. Researchers first learned this species exhibited migratory behavior in 1906 when many washed up on the shores of Lake Huron after an autumnal storm (Saunders 1907). It is now widely recognized that large numbers of Northern Saw-whet Owls move south from breeding areas each fall, traveling as far south as Alabama, Louisiana, and northern Florida (Rasmussen et al. 2008). This autumn exodus is presumably undertaken to escape challenging winter conditions and to find a more stable resource base (Cheveau et al. 2004).

D. F. Brinker and colleagues created Project Owlnet (www.projectowlnet.org) to network a small group of banding stations in eastern North America. Project Owlnet has grown into a nationwide organization for coordinating and standardizing Northern Saw-whet Owl (NSWO) banding methodology. Currently, >125 NSWO banding stations allied with Project Owlnet monitor this species' migration annually (Huy 2010).

These banding stations report time windows during which the majority of Northern Saw-whet Owls are caught in a season. These windows tend to occur later at southern stations than northern stations (Holroyd and Woods 1975, Weir et al. 1980, Brinker et al. 1997). Banding efforts have also revealed that some Northern Saw-whet Owl populations have cyclical migration irruptions about every 4 years. These irruptions are likely due to periods when prey abundance is followed by scarcity, implied by exceptionally high numbers of Northern Saw-whet Owls captured in the fall compared to 'normal' years (Davis 1966, Brinker et al. 1997, Whalen and Watts 2002, Brittain et al. 2009). Banding information has begun to illuminate age-differentiated migration trends in Northern Saw-whet Owls. Juvenile owls may migrate earlier than adults in some areas, and the age ratio of banded owls varies greatly among years and locations (Paxton and Watts 2000, Stock et al. 2006, Brittain et al. 2009).

Our knowledge of Northern Saw-whet Owl migration is clearly limited by the scale of previous research. Virtually all publications have been local or regional, often analyzing data from one or two banding stations. The only study in eastern North America using data from >six stations is 36 years old and limited by the number and distribution of banding stations available at that time (Holroyd and Woods 1975). Over 160,000 Northern Saw-whet Owls have been banded since Holroyd and Woods (1975) published their findings. This rigorous banding effort has generated an extensive data base archived at the U.S. Geological Survey's Bird Banding Laboratory (BBL) that has remained unexplored in eastern North America.

Our objectives were to use the BBL data base to explore multiple questions. (1) Does the timing and direction of the migration front reported in regional studies exist across eastern North Amer-

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ica? (2) Do Northern Saw-whet Owls exhibit inter-annual migration-route fidelity? (3) Do large-scale age-differentiated movement patterns exist? Answering these questions at this novel scale will expand the Northern Saw-whet Owl information portfolio and illustrate the versatility of collective data sets.

METHODS

Data Source, Study Area, and Data Preparation.—We assessed movement patterns using the BBL data base of 170,468 Northern Saw-whet Owl banding events and 2,741 reports of subsequent encounters with banded owls (here after, ''recapture'' will be used for owls encountered post-banding, dead or alive). We examined information from 81,584 Northern Saw-whet Owls banded in 1999–2008 during fall migration between 1 September and 31 December. We assumed this parsing would ensure that nearly all records represented migrating owls. Excluding pre-1999 records ensured that most owls were banded using the audio lure mist-netting technique described in Erdman and Brinker (1997). Records exist across North America, but data west of the Mississippi River are geographically disparate and small in sample size. Thus, we restricted the analyses to records from eastern North America.

Data Analysis.—The BBL reports banding events as either the exact latitude and longitude of the banding location, or the corner coordinates of the 10-minute or 1-minute block that a station falls within. The data base does not report station or bander names, so it is not possible to match all banding event coordinates exactly to banding stations indicated by Project Owlnet (Huy 2010). Thus, we define a 'banding station' as any coordinate where at least one Northern Saw-whet Owl was banded. A 10-minute block is <20 km wide, so the variation in banding coordinate precision is negligible at the scale of eastern North America.

We used a geographic information system (GIS) to draw vectors between banding and recapture locations for each individual captured multiple times, and calculated the spherical lengths of each vector. Compass bearings for each vector were calculated using a Standard Mercator projection designed to represent the line between any two points on a sphere as a constant azimuth. Vectors do not necessarily follow the migration path, but are sufficient for understanding overall distance and direction-of-travel between banding and recapture locations. All spatial analyses were performed using ArcView 9.3® (ESRI 2008).

Migration Timing.—We subdivided eastern North America into lateral bars 01° latitude in width (Fig. 1). We aggregated all banding events by these bars and calculated the mean Julian banding day at each bar. The 01° bars were chosen for convenience and were sufficiently wide to each contain a representative number of banding events. We verified that the mean banding day at each latitude bar coincided with a peak in migration activity represented by a bell curve in frequency distribution of banding days. There was a unimodal Gaussian distribution at all except four latitude bars south of Virginia. These four bars were ultimately excluded from analysis due to small sample size. Mean banding day was graphed against latitude bar, and against the latitude of banding stations with >50 banding events. We used linear regression to assess the strength of these relationships. Similar analyses were conducted to assess differences between adult and juvenile owl movements. Mean banding days for each latitude bar were compared using Chi-square contingency tables. All analyses performed using 01° latitude bars were also performed in the same manner and over the same area using 01° longitude bars to simultaneously identify east-west movement patterns.

We modeled migration timing in eastern North America by performing surface interpolations based on mean banding days at banding stations with >50 banding events. The model used inverse-distance weighting (ESRI 2008) of mean banding days at stations within a fixed-distance neighborhood around each predicted raster cell defined as an ellipse of 1.5° latitude and 05° longitude in radius (power = 1). The search neighborhood was restricted in latitude to limit bias of stations unevenly distributed far north or south of a given cell. The search neighborhood longitude was selected to restrict influence of distant stations while being sufficiently inclusive to interpolate the entire surface.

Variation in banding effort among stations cannot be calculated with the BBL data base. We normalized for banding effort where possible by comparing proportional values among stations rather than using raw totals, or aggregating data by latitude bar instead of banding station.

We estimated migration speed by plotting distance between banding and recapture over time

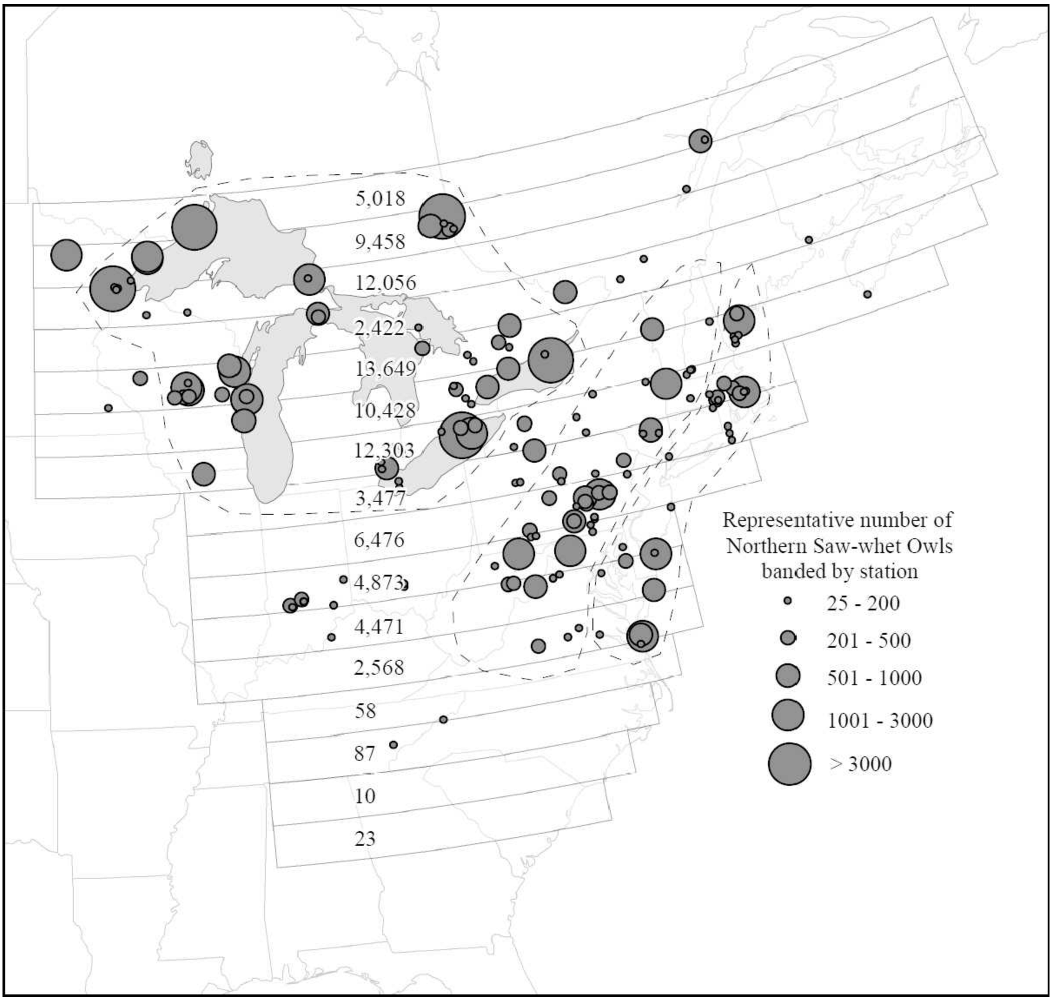

FIG. 1. Northern Saw-whet Owl banding stations in eastern North America, 1999–2008. Bars are 01° latitude in width and used to group banding events for timing and age-differentiated analyses. Labels show the number of banding events within each bar. Dashed lines define the Great Lakes Basin, Appalachian Mountains, and Atlantic seaboard regions compared in directionality and route fidelity analyses.

for Northern Saw-whet Owls captured twice in the same season. We used the slope of the line-of-best-fit to approximate average speed.

Route Fidelity.—We predicted a species with high migration route fidelity would demonstrate low longitudinal deviation with respect to seasonal latitudinal position, i.e., the longitude at which an owl crosses a given latitude during migration would be similar among years. The longitudinal distance between the two locations would represent route deviation. Thus, if migrating owls maintain high route fidelity, they should not be recaptured long distances east or west within a single latitude bar from banding location. Longitudinal deviation and recapture records have been used for assessing migration route fidelity in other species (Rimmer and Darmstadt 1996, Alerstam et al. 2006). Thus, we chose to examine migration route fidelity by isolating from the data base all owls recaptured within 0.5° latitude of their banding location at least 1 year after banding. We consider a 0.5° latitude window sufficiently conservative to accurately represent route deviation while controlling for spurious influence of latitudinal position, i.e., we assume longitudinal route position may change with latitudinal movement; the narrower the latitude bar the more reliable the assessment. We ascertained overall route fidelity by examining the frequency distribution of the banding-to-recapture distance for each owl. We explored general regional differences in route fidelity by analyzing fidelity separately for owls banded in the Great Lakes Basin, the Appalachian Mountains, and the Atlantic seaboard. These regions are defined inexactly (Fig. 1), but are sufficient for making broad comparisons in Northern Saw-whet Owl movements among regions. We used Chi-square contingency tests to ascertain if differences in fidelity exist among regions or among regions and all owls.

Migration Direction.—We generated rose diagrams (Kovach Computing Services 2010) to calculate the mean azimuth and angular distribution of all banding-to-recapture vectors of Northern Saw-whet Owls captured at different stations in the same migration season. Additional rose diagrams were generated that considered owls recaptured >100 or >500 km from banding location to assess the possible influence of owls being recaptured disproportionately among proximate stations (thereby influencing overall angular distribution). We analyzed regional differences in directionality by isolating owls banded around the Great Lakes Basin, in the Appalachian Mountains, or along the Atlantic seaboard and recaptured >100 km from banding location (Fig. 1). We compared the mean directionality among these groupings using pair-wise Watson-Williams *F*-tests described in Fisher (1993).

Age-differentiated Migration.—We tested whether spatial differences exist between adult and juvenile movement patterns. We aggregated banding events into 01° latitude bars and calculated the age ratio of the owls within each bar. Linear regressions were used to assess the strength of the relationship between age ratio and latitude bar. This was done across all years (1999–2008) and independently for each year to reveal differences in movement patterns between irruption and non-irruption years.

We examined spatial differences in migration by performing a surface interpolation of the age ratio of Northern Saw-whet Owls at banding stations with >50 banding events. The interpolations used inverse-distance weighting (ESRI 2008) of age ratios at banding stations within a 3° search radius around each predicted raster cell (power = 2). This search neighborhood restricts the influence of distant stations while being sufficiently inclusive to interpolate the entire surface. This was done for all owls and separately for irruption and non-irruption years. We compared mean banding latitude by age class of all migrating Northern Saw-whet Owls using Wilcoxon Rank-Sum tests. This was done with pooled data (1999–2008) and separately by years.

We examined whether proportions of adults versus juveniles differed among years using Chi-square contingency tests, followed by a *post-hoc* analysis of means for proportions to identify which years were significant deviants (SAS Institute Inc. 2010).

RESULTS

We reviewed information on 81,584 Northern Saw-whet Owls banded in eastern North America during fall migration (1 Sep to 31 Dec) 1999–2008. Banding information was provided by 356 banding stations, 132 of which reported >50 banding events. Twenty stations reported 58% of all banding events (Fig. 1). Forty-five percent of the 81,184 banding events (of 81,584 total) with assigned age were adults and 55% were juveniles. There were 2,184 owls recaptured during fall migration. Seventy-three (3.3%) of these were recaptured >1,000 km from the original banding site.

Migration Timing.—There was a clear trend of northern banding events occurring earlier in the migration season than southern banding events (Fig. 2). The mean ± SD banding day at each latitude bar was 3.8 ± 2.7 days later than the bar immediately north of it. Mean banding day was not significantly different at any latitude bar among juveniles, adults, and all Northern Saw-whet Owls ($\chi^2_{22} = 0.03$, $P > 0.95$). The average difference between adult and juvenile mean banding day at each latitude was 1.2 days (range = 0.17–2.88). Surface interpolation of predicted mean banding day revealed a similar north-south trend with earlier means occurring consistently farther north than later means (Fig. 3). The earliest mean banding days were predicted for eastern Ontario and Quebec, and progressed gradually southward. The latest mean banding days were in Virginia, Delaware, West Virginia, and Indiana, although the interpolation was not performed farther south due to the lack of banding stations and few records in that region.

Northern Saw-whet Owls moved ~10.5 km per night on average (Fig. 4). The line-of-best-fit of mean migration speed was drawn using owls

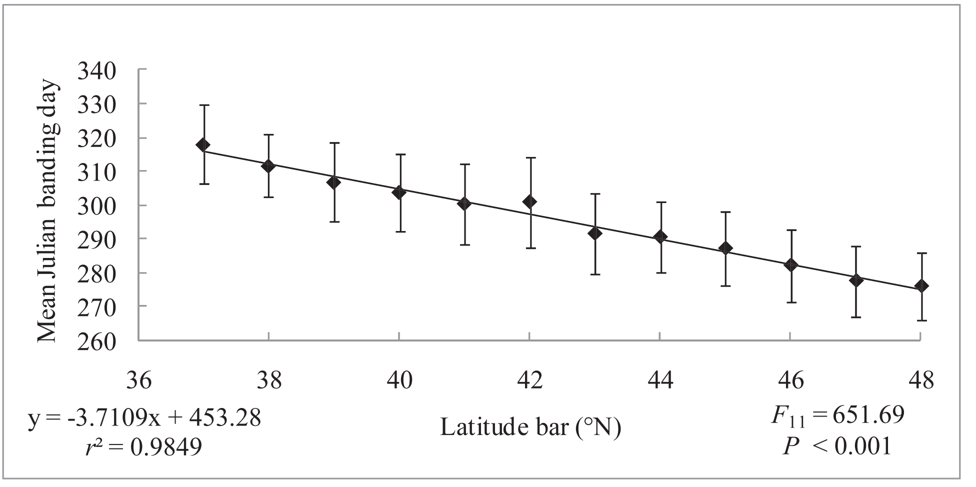

FIG. 2. Seasonal timing by latitude of Northern Saw-whet Owl migration across eastern North America 1999–2008 based on 81,584 banding events grouped into 01° latitude bars. Diamonds show mean ± SD banding day for each latitude bar. Reference Julian days: 1 October = 274; 1 November = 305.

banded and recaptured ≤33 nights apart because there were insufficient same-season recapture data >33 days to accurately represent migration speed at longer time intervals.

Migration Route Fidelity.—Seventy-two percent of 512 Northern Saw-whet Owls whose route deviation could be assessed (recaptured >1 year after banding within 0.5° latitude of banding location) were recaptured within 100 km east-west of their banding location. Thirty-four percent were recaptured within 20 km. The individual deviating farthest from its previous migration route was recaptured 981 km from its banding location. Forty-one percent of the data was represented by individuals banded and recaptured at two proximate stations west of Lake Michigan. We removed individuals encountered at these stations to isolate their effect on the overall analysis. The difference in results was statistically significant ($\chi^2_4 = 30.34$, $P < 0.001$); however, removal of these stations resulted in an increase in route fidelity (Table 1).

There was no significant difference in route fidelity measures among owls banded in the Great Lakes Basin, Appalachian Mountains, and Atlantic seaboard regions ($\chi^2_9 = 9.08$, $P = 0.33$, Table 1). There were no significant pair-wise differences between all owls and regional groupings ($\chi^2_4 < 8.16$, $P > 0.09$).

Migration Direction.—Mean ± SD vector azimuth of 688 Northern Saw-whet Owls banded and recaptured at different locations during the same fall migration was 191.5 ± 3.8° and statistically similar ($F_1 = 0.16$, $P = 0.689$) to owls banded and recaptured >100 km apart (Fig. 5A, B). Significantly different ($F_1 = 13.74$, $P < 0.001$) south-southeastern movement was found in owls banded and recaptured >500 km apart (Fig. 5C). Eight percent (8.2%) of owls banded and recaptured at different locations were recaptured north of where they were banded; 4.4% of northbound owls were recaptured >100 km from banding location, and none was recaptured >500 km distant.

There was a significant difference in directionality among all owls recaptured >100 km from banding site and all three regional groupings ($F_1 > 4.26$, $P < 0.04$, Fig. 5B, D–F). There was a significant difference in mean directionality among owls banded in the Great Lakes Basin versus those banded in the Appalachian Mountains ($F_1 = 11.54$, $P < 0.001$ Fig. 5D, E) and the Atlantic seaboard ($F_1 = 25.00$, $P < 0.001$, Fig. 5D, F). There was no difference in mean directionality among owls banded in the Appalachian Mountains region and the Atlantic seaboard region.

Age-differentiated Migration.—Proportions of adults versus juveniles differed significantly among years ($\chi^2_9 = 5{,}071.01$, $P < 0.0001$). Years 1999, 2001, 2003, 2006, and 2007 were significant deviants below the overall mean proportion. All other years were significant deviants above the overall mean proportion (Table 2).

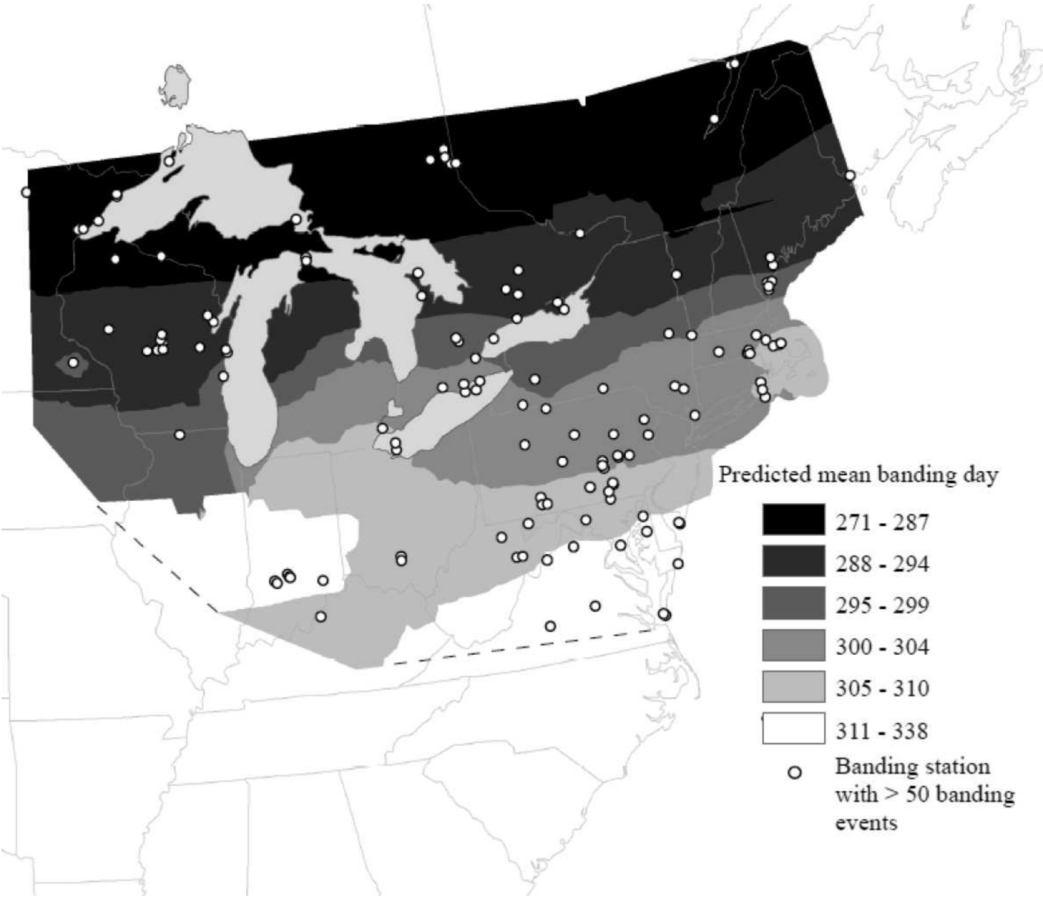

FIG. 3. Predicted fall migration timing of Northern Saw-whet Owls across eastern North America based on mean banding day at 132 stations with >50 banding events, 1999–2008. Calculated by inverse-distance weighted interpolation that considers stations within a 1.5° latitude and 05° longitude radius ellipse around each raster cell. Reference Julian dates: 1 October = 274; 1 November = 305. Dashed lines represent interpolation boundary.

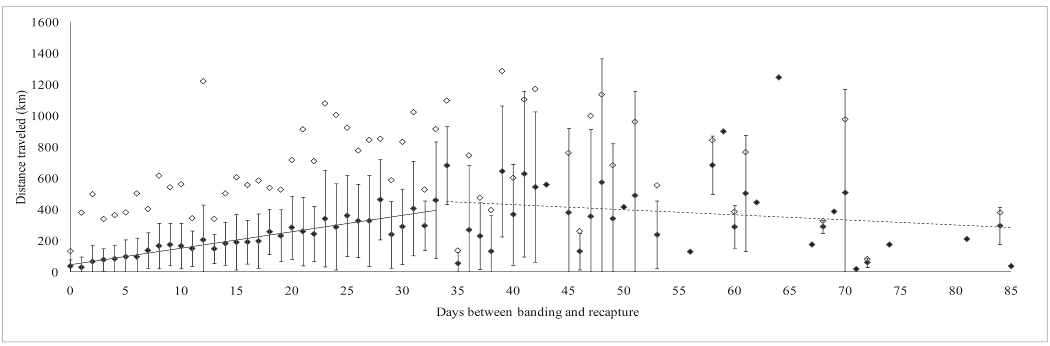

FIG. 4. Mean ± SD (solid diamonds) and maximum distance (hollow diamonds) traveled by 915 Northern Saw-whet Owls recaptured x days after banding. The solid line-of-best-fit shows the trend in mean distance traveled from 0 to 33 days ($y = 10.5x + 47.7$, $r^2 = 0.85$, $P < 0.001$, $n = 825$). The dashed line-of-best-fit shows the trend in mean distance traveled from 34 to 85 days ($y = -3.3x + 562.7$, $r^2 = 0.03$, $P = 0.28$, $n = 90$). Separate trend lines were presented to reveal that the time-distance association appears to break down after ~33 days.

TABLE 1. Migration route deviation in Northern Saw-whet Owls recaptured within 0.5° latitude from banding location >1 year after banding. 'Distance' represents straight-line distance between banding and recapture locations. A large proportion of same-site recaptures occurred at two sites west of Lake Michigan. We present a truncated data column that does not include information from these two sites to examine their effect on the overall trend. Further information is presented for owls banded within specific regions. The two sites west of Lake Michigan are excluded from the 'Great Lakes' group.

	All owls (n = 512)		Truncated data (n = 312)		Great Lakes (n = 161)		Appalachian Mountains (n = 41)		Atlantic seaboard (n = 50)	
Distance (km)	n	%	n	%	n	%	n	%	n	%
≤20	174	33.9	161	51.6	66	40.1	12	29.3	34	68.0
≤50	334	65.5	202	64.7	95	59.0	15	36.5	40	80.0
≤100	368	72.2	230	73.7	107	66.5	25	61.0	44	88.0
≤300	487	95.0	291	93.2	47	91.3	38	92.7	48	96.0
≥301	25	4.9	21	6.7	14	8.7	3	7.3	2	4.0

There was no significant relationship between adult: juvenile ratio and latitude for all years combined (n = 81,184, r^2 = 0.008, P = 0.77, Fig. 6). The relationship was significant in irruption year 2003 and non-irruption years 2006 and 2008, when tested separately by year. The relationship was insignificant and in inconsistent directions in 7 of 10 years (Table 3). There was no significant difference in adult versus juvenile mean banding latitude for all years combined (P = 0.46, Table 2). There was a significant difference in 9 of 10 years when tested separately, but the differences were not in a consistent direction.

Surface interpolation of age ratios showed areas of predicted high and low values (Fig. 7), but these areas were patchy and localized. Highest adult: juvenile ratios were predicted in Wisconsin, Virginia, northern New England, and New York. Lowest adult: juvenile ratios were predicted in eastern Ontario north of Lake Huron, eastern Quebec, around Lake Erie, and at coastal stations in Massachusetts, Rhode Island, New Jersey, and around Chesapeake Bay (Fig. 7A). Results were similar in irruption years (Fig. 7B), but with lower overall ratios across the surface. Results for non-irruption years were similar to the interpolation for all owls (Fig. 7C), but with highest adult: juvenile ratios also occurring across Virginia, West Virginia, Kentucky, and Indiana.

DISCUSSION

Migration Timing.—Peak migration activity occurred progressively southward over the course of the season, suggesting that Northern Saw-whet Owls migrate in distinct fronts. This trend is consistent using multiple analyses, indicating the strength of this trend and the reproducibility of the results (Figs. 2–3). This supports the southbound trend that researchers have supposed for decades based on the accretion of regional observations (Mueller and Berger 1967, Weir et al. 1980, Erdman et al. 1997, Brittain et al. 2009). We could expect a less-striking latitudinal gradient and more irregular distributions of the owls banded at each latitude if Northern Saw-whet Owls were moving southward haphazardly over the entire migration season. The observed trend implies that fall migration is uniform and not a random seasonal dispersal in search of better resources.

Our results closely match those of Holroyd and Woods (1975), the only other study that compares mean Northern Saw-whet Owl capture dates among multiple banding stations in eastern North America. The distribution of banding dates for most of their study regions were within our predicted means (Fig. 3). Our predicted means for Massachusetts, Maryland, and New Jersey were 1–2 weeks later than indicated in Holroyd and Woods (1975). Mean banding day in Ontario was predicted ~1 week earlier than they indicated. This inconsistency may be due to varying weather patterns, shifts in population centers that change migration distances or the small sample size (n = 4,802) available for their study. The overall similarity in results despite the >30 year difference in sampled populations (1955–1969 in theirs vs. 1999–2008 in ours) shows the long-term temporal consistency of this species' fall migration. This similarity also shows these results may be reproducible using other methodologies. The abrupt late mean banding day predicted in central Illinois may be explained by low banding station density in that area. This area may reveal

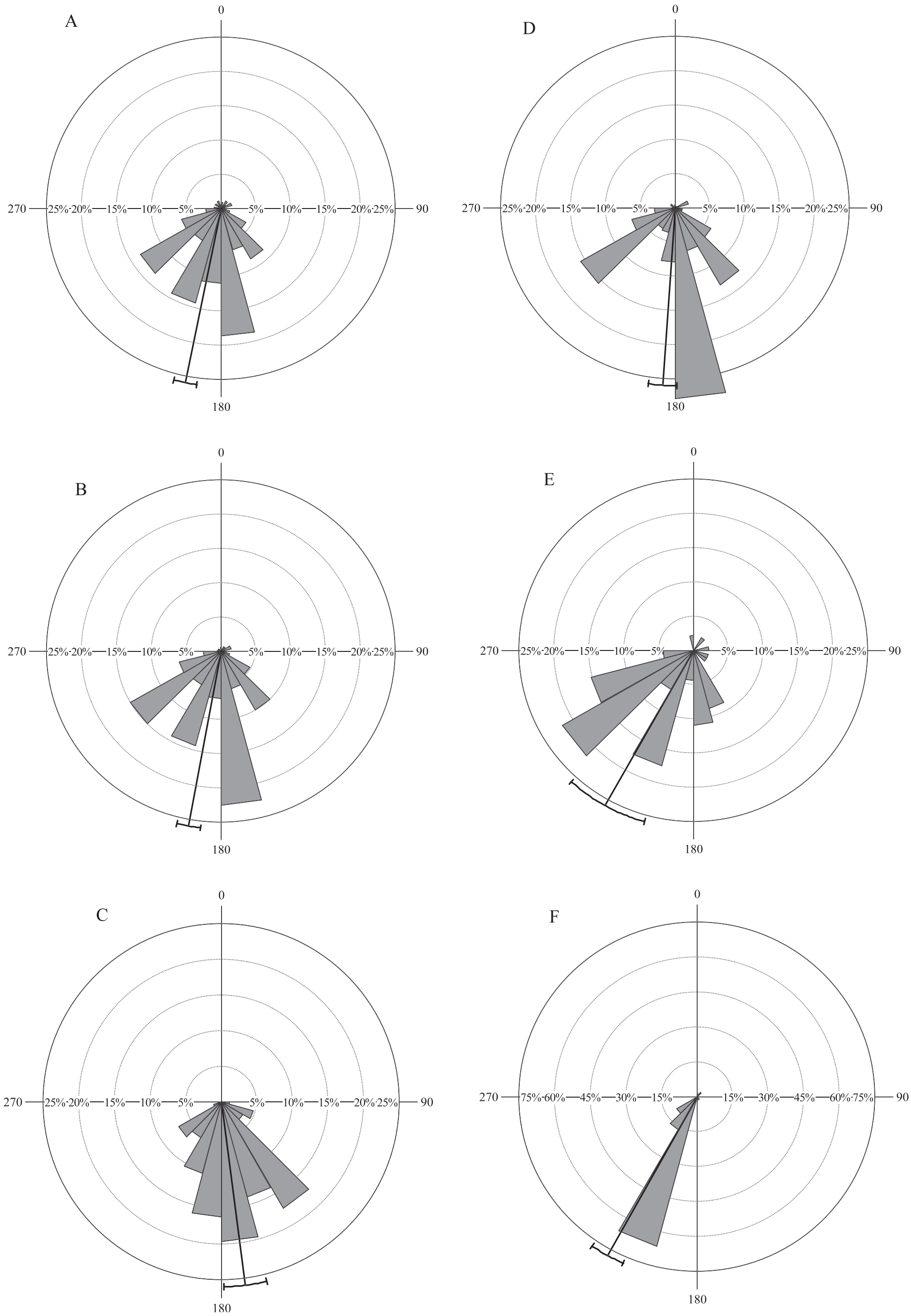

FIG. 5. Directional movement of Northern Saw-whet Owls in eastern North America during fall migration, including mean compass bearing and 95% confidence interval (indicated by black line and cross-bar), 1999–2008. Rose wedge lengths and axis labels indicate percentage of total within that azimuth bin. A = the angular distribution of banding-to-recapture vectors of 688 Northern Saw-whet Owls banded and recaptured in the same season (mean = 191.5 ± 3.8°). B = distribution of 549 owls recaptured >100 km from banding location (mean = 190.4 ± 3.8°). C = distribution of 87

TABLE 2. Adult and juvenile proportions by year (1999–2008), and one-way analysis of mean adult banding latitude versus mean juvenile banding latitude of Northern Saw-whet Owls in eastern North America (Wilcoxon Rank-Sum tests).

Year	Adult *n* (%)	Juvenile *n* (%)	Mean ± SE adult banding lat. °N	Mean ± SE juvenile banding lat. °N	Wilcoxon *Z*	*P*
1999	3,378 (32)	7,298 (68)	43.33 ± 0.05	42.56 ± 0.04	11.83	<0.0001
2000	3,553 (60)	2,320 (40)	44.10 ± 0.04	44.63 ± 0.05	8.27	<0.0001
2001	2,929 (41)	4,067 (59)	43.33 ± 0.05	42.50 ± 0.05	12.61	<0.0001
2002	3,220 (53)	2,894 (47)	43.76 ± 0.04	44.24 ± 0.05	6.21	<0.0001
2003	3,686 (40)	5,590 (60)	43.75 ± 0.09	44.22 ± 0.04	−6.21	<0.0001
2004	4,743 (58)	3,449 (42)	43.36 ± 0.04	43.73 ± 0.05	5.56	<0.0001
2005	4,268 (51)	4,060 (49)	44.19 ± 0.04	44.18 ± 0.05	0.26	0.79
2006	2,645 (37)	4,540 (63)	44.69 ± 0.05	45.47 ± 0.04	−13.12	<0.0001
2007	4,543 (32)	9,659 (78)	43.27 ± 0.04	43.16 ± 0.03	2.28	0.02
2008	3,267 (75)	1,076 (25)	43.26 ± 0.05	44.70 ± 0.09	12.20	<0.0001
Totals	36,231 (45)	44,985 (55)	43.67 ± 0.02	43.69 ± 0.02	−0.74	0.46

limitations in all interpolation modeling to predict values in regions with few or no sampling points.

Banders may begin trapping in response to reports through Project Owlnet of banding success at more northern stations. Thus, the calendar of Northern Saw-whet Owl banding events in this study may conceivably be influenced by Project Owlnet, and this influence may bias the results. However, we observed a Gaussian distribution of banding events at each latitude bar (Fig. 2) demonstrating that a sufficient sampling of owl movement is achieved despite the potential timing biases associated with Project Owlnet communication. We suspect most banders anxiously wait for migration to begin each season and open nets well before more-than-meager numbers arrive, e.g., 1–2 owls/night. If anything, Project Owlnet improves the accuracy of our seasonal timing assessment.

The average speed (10.5 km/day, Fig. 4) was slower than the speed of individuals reported in other studies (14–32 km/day in Virginia, Brinker et al. 1997; 20–30 km/day in Wisconsin, Erdman et al. 1997; 28.8 km/day in Indiana, Brittain et al. 2009; 37 km/day in Alberta, Priestley et al. 2010). However, if we assume that each degree of latitude in our study is ~111 km, the progression of the peak banding window (Fig. 2) indicates the migration 'front' moves ~30 km/day. The discrepancy between these two rates may be because the migration 'front' is a measure of fluid population movement, while the migration speed analysis (Fig. 4) represents individual movements including stopovers (Whalen and Watts 2002) not reflected in the measurement of overall population movement. The fastest records (Fig. 4) demonstrate that Northern Saw-whet Owls are capable of sustained movement even if normal migration behavior includes frequent stopovers.

Migration Route Fidelity.—Catry et al. (2004) argue that migrant passerines rarely exhibit route and stopover-site fidelity because they are solitary, short-lived, and highly terrestrial (and therefore have more potential stopover sites than other types of birds). Their energetically costly flight style also hinders correction for wind drift. These qualities are true for Northern Saw-whet Owls as well, but our findings suggest this species may be generally faithful to migration routes. Seventy-two percent of owls recaptured >1 year after banding ±0.5° latitude from banding location were recaptured <100 km from their banding locations (Table 1), suggesting that individuals follow similar migration routes among years.

The Great Lakes may characterize geographic barriers that could constrict Northern Saw-whet Owl movement and cause a migratory bottleneck.

←
owls recaptured >500 km from banding location (mean = 172.5 ± 6.8°). D = distribution of 381 owls banded in the Great Lakes Basin and recaptured >100 km from banding location (mean = 184.9 ± 4.8°). E = distribution of 46 owls banded in the Appalachian Mountains region and recaptured >100 km from banding location (mean = 209.2 ± 13.4°). F = distribution of 80 owls banded along the Atlantic seaboard and recaptured >100 km from banding location (mean = 184.0 ± 4.6°).

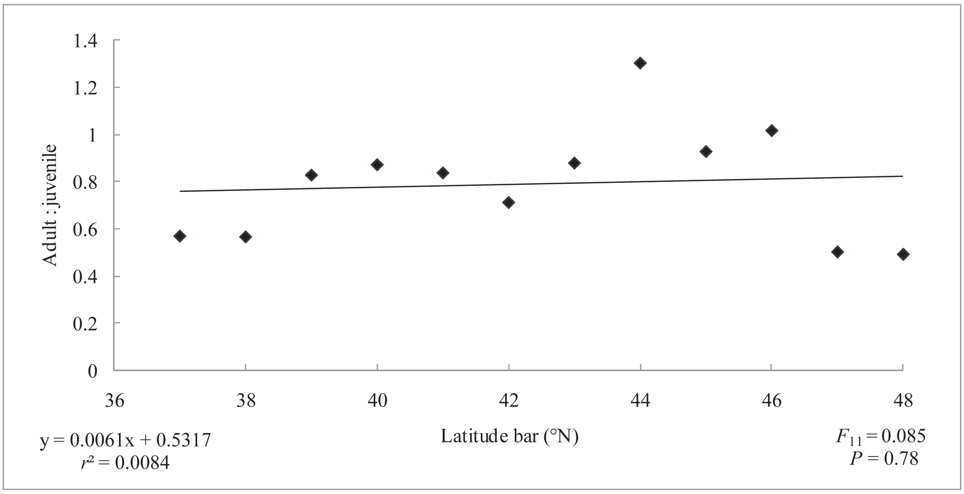

FIG. 6. Age-differentiated distribution by latitude of Northern Saw-whet Owl banding events during fall migration across eastern North America, based on 81,184 banding events, 1999–2008, grouped into 01° latitude bars.

This type of funneling may explain why 41% of owls in our fidelity analysis were banded and recaptured at two stations west of Lake Michigan. It may be argued this potential geographic funneling biases fidelity estimates. However, similar circumstances of restricted movement would be required throughout the year to challenge migration route fidelity estimates. Clearly, there was ample opportunity for these individuals to move southward along the other side of the lake or to take a different route void of the Great Lakes influence. Consistent repeated movement along the same corridor during fall migration, constricted or not, is a valid assessment of route fidelity. It is possible that some owls encountered at these two sites were residents, but similar fidelity measures were found in the Great Lakes Basin when these stations were removed, and in regions where few resident owls are present (Rasmussen et al. 2008). The lack of significant difference in fidelity measures among the Great Lakes Basin and other regions suggests that geologic constraints do not fully explain the high route fidelity indicated by our analysis. High fidelity was observed in the Appalachian Mountains where movement is unlikely restricted by geologic features, but may be selected for structural and resource benefits, showing that Northern Saw-whet Owls may follow consistent routes where geographic bottlenecks are not present.

Our study addresses migration route fidelity rather than nesting-site fidelity, but our results contribute to the ongoing discussion of nomadic behavior in Northern Saw-whet Owls (Marks and Doremus 2000, Bowman et al. 2010). Our

TABLE 3. Linear relationship between adult-to-juvenile ratio (y) and latitude bar (x) for Northern Saw-whet Owls in each year, 1999–2008.

Year	y =	r^2	F	df	P	n
1999	0.009x + 0.012	0.027	0.277	11	0.61	10,676
2000	−0.146x + 8.124	0.268	3.657	11	0.085	5,873
2001	0.037x − 0.894	0.118	1.335	11	0.275	6,995
2002	−0.054x + 3.386	0.233	3.04	11	0.112	6,114
2003	−0.042x + 2.473	0.414	7.066	11	0.024	9,276
2004	−0.026x + 2.542	0.058	0.617	11	0.45	8,192
2005	0.019x + 0.280	0.066	0.712	11	0.419	8,328
2006	−0.039x + 2.373	0.398	5.950	10	0.037	7,185
2007	0.027x − 0.556	0.076	0.826	11	0.385	14,202
2008	−0.766x + 36.943	0.740	29.770	11	0.0003	4,343

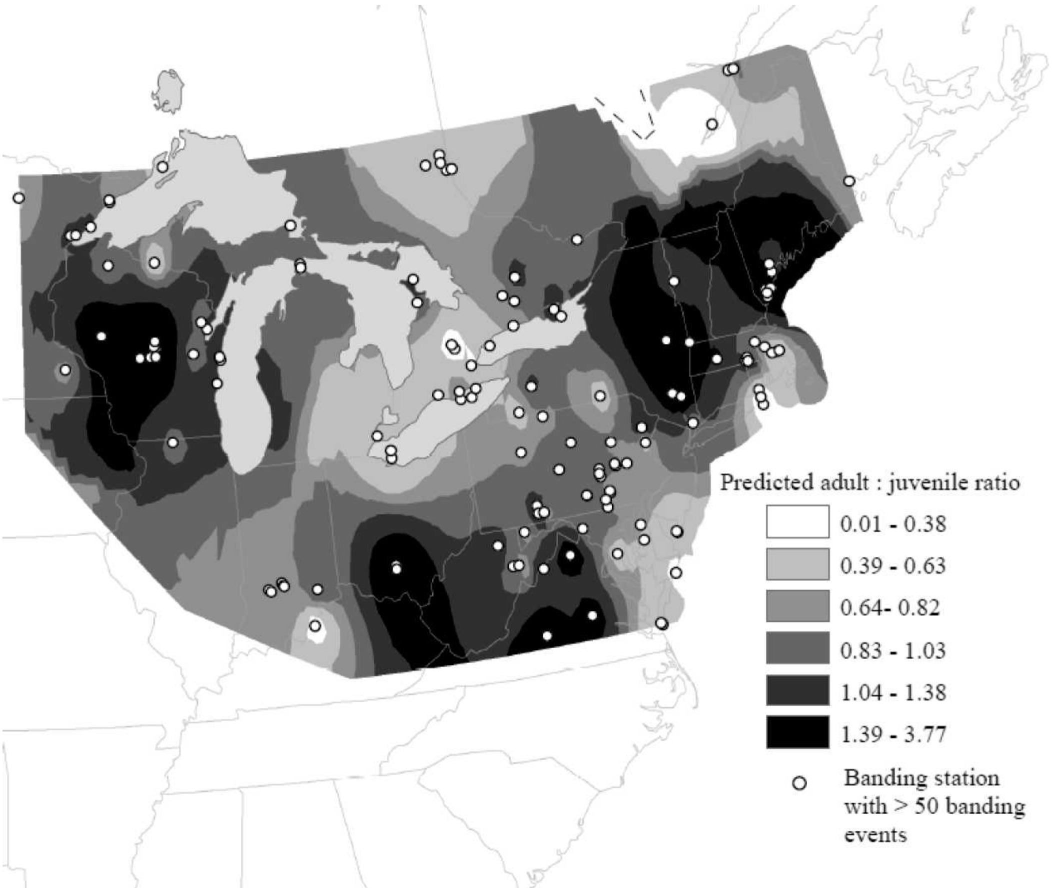

FIG. 7A = predicted age distribution of migrating Northern Saw-whet Owls in eastern North America, 1999–2008, based on age ratios at 132 stations with >50 banding events. 7B = predicted age distribution of owls at 89 stations in irruption years. 7C = predicted age distribution of owls at 101 stations in non-irruption years. Interpolation uses inverse-distance weighting of adult: juvenile ratios at banding stations within a 3° radius around each predicted raster cell. Dashed lines represent interpolation boundary.

analysis indicated that many owls are banded in high-latitude breeding regions and recaptured nearby in subsequent years. This suggests that some owls may consistently travel from historical breeding areas and maintain high migration route fidelity. For example, if a bird is repeatedly captured at the same site in Wisconsin in different years during migration, it is more likely to have bred repeatedly in the western Great Lakes Basin than in eastern Quebec. Thus, although Northern Saw-whet Owls may only rarely reoccupy the same breeding territory (Marks and Doremus 2000), they may still remain regionally faithful.

Marks and Doremus (2000:302) noted ''the best evidence for nomadism would be the capture of marked individuals at widely separated breeding sites in different years,'' yet a decade later there is still limited banding effort during the breeding season, and insufficient data to fully understand the scale of nomadism in Northern Saw-whet Owls. We conclude, based on the level of migration route fidelity found in this study, this species has ordered movement during migration and is not moving haphazardly in search of food.

Migration Direction.—Our results show a clear southbound movement pattern indicated by the directional distribution of Northern Saw-whet Owls banded and recaptured in the same migration season (Fig. 5). Most studies assume a southward migration based on the accumulation of southbound movement via recapture reports in their study areas (Brinker et al. 1997, Erdman et

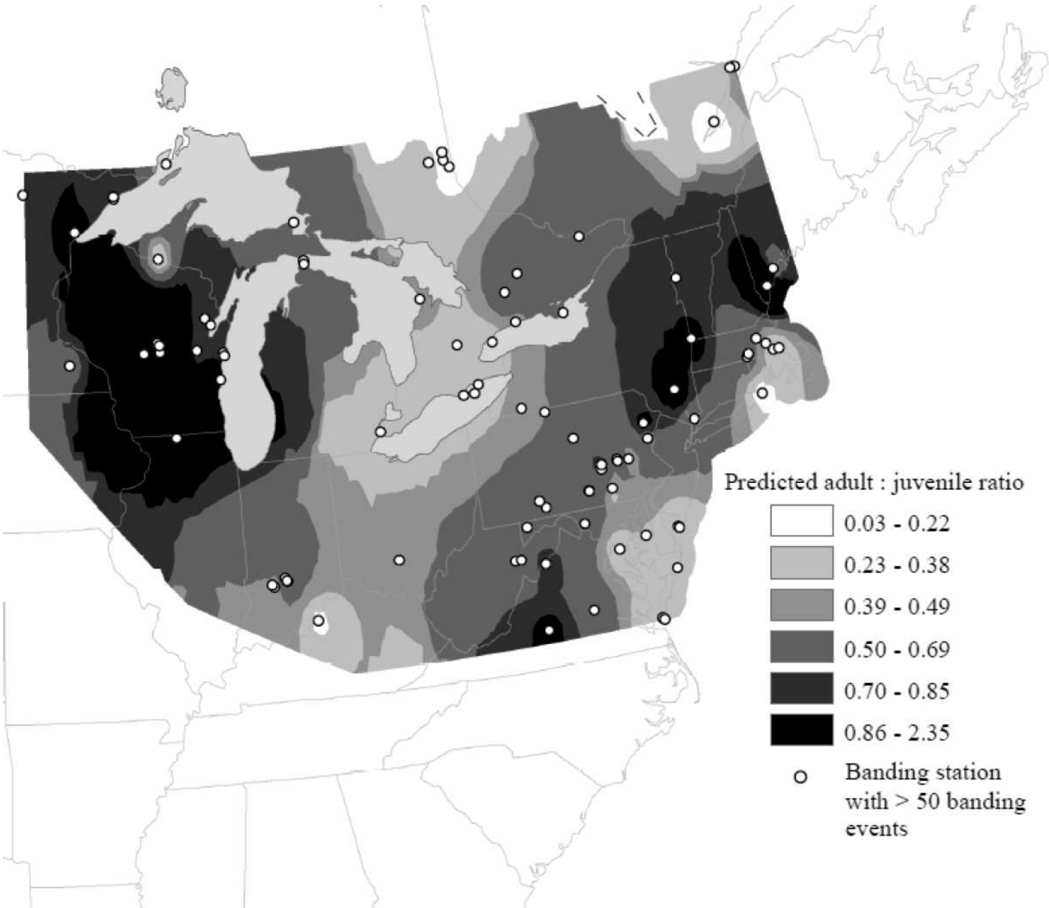

FIG. 7B. Continued.

al. 1997, Brittain et al. 2009), but this is the first study to quantify the directionality of fall migration in this species using large-scale recapture data.

The results also reveal the frequency of northbound movement. Local studies emphasize northbound individuals when summarizing recapture information (Holroyd and Woods 1975, Erdman et al. 1997, Marks and Doremus 2000), and this may give the impression the overall migration direction is more random. However, northbound individuals comprise a small percentage of same-year recaptures (Fig. 5). Fall movements in non-southbound directions should be considered exceptions to the general southward migration trend. The similar southward mean azimuths and narrow confidence intervals, regardless of minimum banding-to-recapture distance (Fig. 4B, C), suggests that most directional distribution biases due to encounters among proximate stations are overwhelmed by actual movement patterns.

The uniform directionality distribution of Northern Saw-whet Owls in the Atlantic seaboard region may indicate that migration along the Atlantic seaboard is restricted by the coastline, and owls are following the coast rather than flying west into the Appalachian Mountains. The wider directional distribution of owls in the Appalachians suggests owls are moving somewhat more haphazardly in that region, possibly guided by the southwest orientation of the mountain range. This is congruent with observations in Alberta of Northern Saw-whet Owl movement guided by the Rocky Mountains and the boreal forest edge (Priestley et al. 2010). This less-uniform migration may be due to the extensive forest cover across the Appalachian range, or due to owls searching for suitable wintering areas after reaching the winter range.

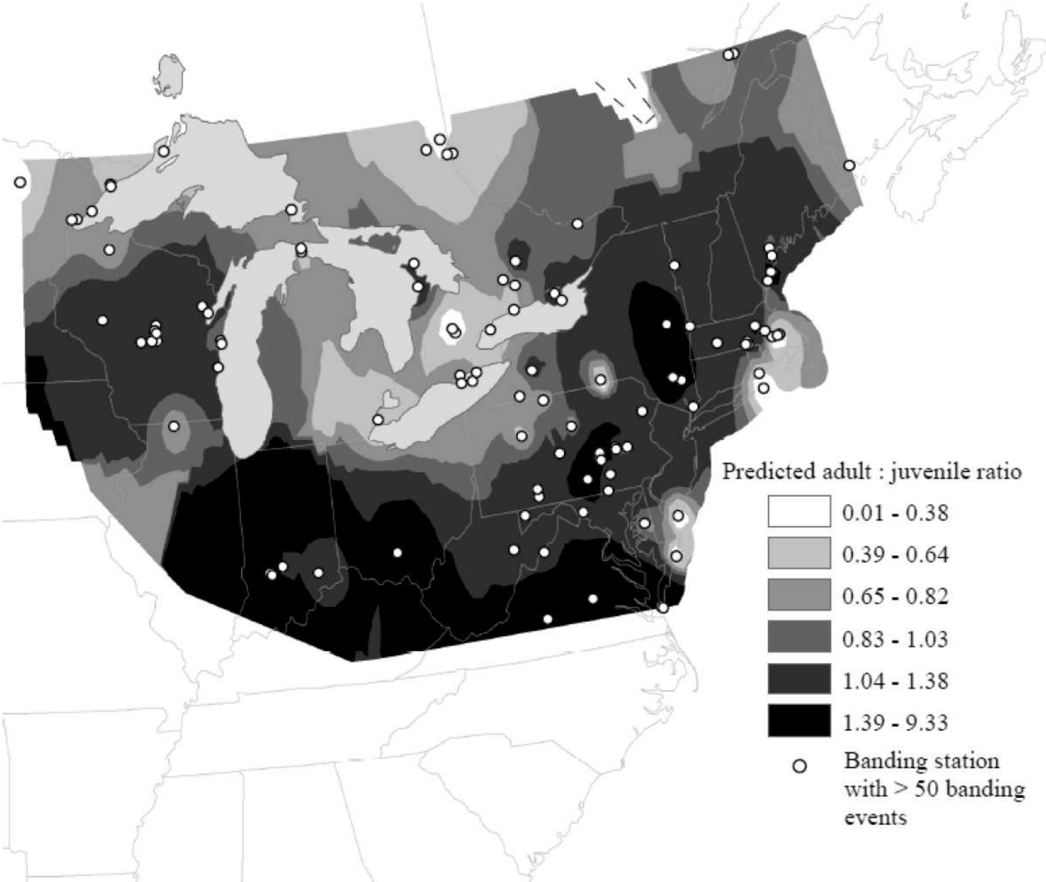

FIG. 7C. Continued.

The wide directionality distribution of migrants in the Great Lakes Basin illustrates that owls traveling through this region have many directional options, supporting our conclusions of high route-fidelity in this region (Table 1).

Overall observed directionality may be influenced by the distribution of banding stations across eastern North America. For example, owls migrating southeast from western Pennsylvania would be more represented in the data base than owls migrating southwest due to the location and number of 'downstream' stations (Fig. 1). Station location biases may explain the significant difference in directionality between owls recaptured >100 versus >500 km from banding location. However, such biases do not obscure our general conclusion that Northern Saw-whet Owls are migrating predominately southward.

Age-differentiated Migration.—Juveniles were banded more frequently than adults, and this is consistent with local studies (Weir et al. 1980, Stock et al. 2006, Brittain et al. 2009). Banders in eastern North America report a striking increase in the proportion of juveniles banded in irruption years (Brinker et al. 1997, Paxton and Watts 2000, Whalen and Watts 2002). Our results support this finding. The percentage of adult Northern Saw-whet Owls was lowest in 1999 and 2007, two well-recognized irruption years, and highest in years immediately following these irruptions (Table 2). This is consistent with local findings as well (Paxton and Watts 2000). The discrepancy in proportions of juveniles is likely due to the cyclical prey base causing high reproductive success in irruption years followed by poor success the following year (Cheveau et al. 2004). Also, many adults in post-irruption years are returning second-year birds that hatched the previous year.

Our results did not reveal unequivocal evidence of age-differentiated migration based on latitude or longitude. Areas of both high and low adult: juvenile ratios occur in the northern and southern extents of our analyses (Fig. 7). The lowest adult: juvenile ratios were in the two northernmost latitude bars, but the highest ratios were in the next three adjacent bars (Fig. 6). By-year regression analysis showed no consistent relationship between age ratio and latitude. Only 3 of 10 years tested had a significant trend, and these were not in a uniform direction (Table 2). Tests of mean banding latitude by age were not significant for all years, and they were not in a uniform direction (Table 3). The direction or significance of these tests is not explained by irruption or non-irruption years. The small mean difference in migration timing between adults and juveniles at each latitude bar does not suggest differential migration timing by latitude.

We did not detect movement patterns explained by latitude, but our interpolations indicate that adult versus juvenile migration is non-uniform across eastern North America (Fig. 7). Juveniles in Idaho had lower body condition scores than adults (Stock et al. 2006). Along the Atlantic Coast, juveniles may arrive on the Delmarva Peninsula almost 2 weeks earlier than adults (Paxton and Watts 2000). Juveniles also benefit less from site familiarity than their parents, and may be less inclined to remain near breeding areas (Côte et al. 2007). These studies imply age-related differences in the ability to cope with challenging conditions, and suggest that juveniles may migrate differently than adults in some areas as a result. The predicted areas of high and low adult: juvenile ratios were similar in both irruption and non-irruption years and support the hypothesis of age-specific preferences for migration routes or wintering sites (Fig. 7B, C). Regionally variable forest structure, prey availability, or climate may influence these preferences, and may explain the patchiness observed in our interpolations. It is possible that resident populations of Northern Saw-whet Owls at high latitudes or high elevations in the Appalachian Mountains are influencing these interpolations (Rasmussen et al. 2008). However, the migration timing interpolation (Fig. 3) and directionality analyses (Fig. 5) showed no clear evidence of resident owls obscuring the overall observed migration pattern, suggesting the impact of residents on the overall data set is minimal.

The quality of any interpolation is limited by the accuracy and distribution of sampling points across the surface. Thus, we refrain from interpreting interpolation results in areas with low station density or areas influenced heavily by one data point. Increased banding efforts in regions with low station density will greatly improve our understating of large-scale migration patterns in this species.

This study is an example for assessing the strength and versatility of using the BBL's large banding data base to understand bird migration. The kinds of information that can be gleaned from banding studies may be limited compared to other techniques, but banding is one of the only tools available for studying cryptic or nocturnal species like Northern Saw-whet Owls. We expand the Northern Saw-whet Owl information portfolio and illustrate the versatility of aggregate data sets as a tool for answering large-scale questions regarding migration by assessing movement patterns beyond published regional trends.

ACKNOWLEDGMENTS

We thank M. A. Cunningham of the Department of Earth Science and Geography at Vassar College for support in designing the analyses. This project would not have been possible without data generated by hundreds of Northern Saw-whet Owl banders who submit their information to the USGS Bird Banding Laboratory; information provided by D. F. Brinker of Project Owlnet, David Okines of Prince Edward Point Bird Observatory, David Evans of the Hawk Ridge Nature Reserve, Eugene Jacobs of Linwood Springs Research Station, Jon McCracken of Thunder Cape Bird Observatory, Bruce Murphy of Hilliardton Marsh, and Scott Weidensaul of The Ned Smith Center for Nature and Art account for 47% of all banding data used in this study. We thank Jennifer Pontius of the University of Vermont for support in statistical analysis. Logistical support was provided by Daniel Bystrak of the Patuxent Wildlife Research Center and associates of Project Owlnet. We thank the Vassar College Environmental Research Institute for financial support of the project.

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