Acoustic monitoring of nocturnally migrating birds accurately assesses the timing and magnitude of migration through the Great Lakes

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RESEARCH ARTICLE

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ABSTRACT

Tracking the movements of migratory songbirds poses many challenges because much of their journey takes place at night. One promising technique for studying migratory birds relies on microphones to record the nocturnal flight calls produced by birds on the wing. We compared recordings of night flight calls with bird-banding data in a southern Great Lakes ecosystem. We collected >6,200 hr of nocturnal recordings at 7 locations around Lake Erie. We detected >60,000 flight calls from migratory birds and classified 45,775 calls to species level or to a bioacoustic category comprising several species with similar calls. We compared these acoustic data with records of 5,624 birds captured in mist nets. We found that acoustic recordings accurately quantified the magnitude of migration; comparison with mist-net data revealed significant positive correlations between the number of acoustic detections and the number of mist-net detections across species. We also found that acoustic recordings accurately quantified the timing of migration; we found significant positive correlations between the date of passage of the 10th, 50th, and 90th percentiles of the populations of up to 25 groups of passage migrant species in the acoustic data and mist-net data. A careful examination of 6 species with distinctive flight calls revealed only subtle seasonal differences between peak detections via acoustic monitoring and mist netting, at both daily and weekly timescales. This research enhances our understanding of the role that acoustic sampling can play in monitoring migratory birds, providing important empirical support for the validity of night-flight-call monitoring.

Keywords: acoustic monitoring, migration monitoring, night flight call, nocturnal vocalizations, population monitoring

El monitoreo acústico de aves que migran en la noche determina de forma precisa el momento y la magnitud de la migración a través de los Grandes Lagos

RESUMEN

Rastrear los movimientos de la aves migratorias impone muchos desafíos puesto que buena parte de su recorrido tiene lugar en la noche. Una técnica promisoria para el estudio de las aves migratorias se apoya en el uso de micrófonos para grabar las llamadas de vuelo producidas por las aves mientras vuelan en la noche. En este estudio comparamos grabaciones de llamadas emitidas durante vuelos nocturnos con datos de anillamiento de aves en un ecosistema del sur de los Grandes Lagos. Recolectamos más de 6,200 horas de grabaciones nocturnas en siete localidades alrededor del lago Erie. Detectamos más de 60,000 llamadas de vuelo de aves migratorias y clasificamos 45,775 llamadas a nivel de especie, o a nivel de una categoría bioacústica que comprende varias especies con llamados similares. Comparamos estos datos acústicos con registros de 5,624 aves capturadas en redes de niebla. Encontramos que las grabaciones acústicas cuantificaron de manera precisa la magnitud de la migración. La comparación con los datos de redes de niebla reveló correlaciones positivas significativas entre el número de detecciones acústicas y el número de detecciones por red de niebla en distintas especies. También encontramos que las grabaciones acústicas cuantificaron de forma precisa el momento en que tiene lugar la migración. Encontramos correlaciones positivas significativas entre los datos acústicos y de redes de niebla en sus estimados de la fecha de paso de los percentiles 10, 50 y 90 de las poblaciones de hasta 25 grupos de especies migratorias. Un examen cuidadoso de seis especies con llamadas de vuelo características indicó que solo existen diferencias estacionales sutiles entre los picos de detecciones obtenidos por monitoreo acústico y por redes de niebla a escala diaria y escala semanal. Esta investigación mejora nuestro entendimiento del papel que puede desempeñar el muestreo acústico en el monitoreo de aves migratorias y provee importante evidencia empírica sobre la validez del monitoreo de llamadas emitidas durante vuelos nocturnos.

Palabras clave: llamadas de vuelo nocturno, monitoreo acústico, monitoreo de la migración, monitoreo de poblaciones, vocalizaciones nocturnas

INTRODUCTION

Obtaining accurate and long-term population trend data on migratory birds is critical for guiding conservation efforts. The inaccessibility of remote habitats in the north temperate zone makes it difficult to monitor many populations of migratory songbirds on their breeding grounds using standard monitoring techniques, such as the Breeding Bird Survey (Dunn et al. 1997). Monitoring the biannual bird migration en route is an efficient means of collecting population data on numerous species from multiple breeding habitats (Millikin 2005).

Current migration monitoring programs (such as the Canadian Migration Monitoring Network) are invaluable for collecting population data on Neotropical migrants at stopover locations along their migration routes. Population estimates from surveys of breeding birds are positively correlated with estimates from surveys during migration, demonstrating that migration monitoring en route represents an accurate tool for studying populations of Neotropical birds (Dunn 2005, Osenkowski et al. 2012). Not only can migration monitoring provide population indices for hundreds of migratory bird species, it can also help us understand movement patterns (Hussell and Ralph 2005); identifying preferred routes and timing of migratory movements has been recognized as a priority for migration research (Faaborg et al. 2010). Furthermore, data on migratory activity of birds at a local landscape level can inform activities such as the placement of communication towers and wind turbines (Evans and Mellinger 1999).

Migration monitoring stations often use several survey techniques in concert, including mist netting, daily walking censuses, and incidental observations (Dunn 2005, Hussell and Ralph 2005). Yet a significant shortcoming of most current migration monitoring techniques is that they are diurnal; birds that migrate at night will be missed by daytime migration monitoring efforts unless the birds stop to spend the day foraging or resting at the stopover site (Dunn 2005). Furthermore, migration monitoring stations are limited to sampling birds in the immediate vicinity of the mist nets or census routes, and population estimates may be influenced by local habitat features or subtle changes in migratory routes (Francis et al. 2009). Moreover, mist netting is a labor-intensive strategy for migration monitoring, often depending on groups of dedicated volunteers and requiring significant training to ensure safe bird handling.

In many bird species, including most songbirds and shorebirds, much of the migratory journey takes place at night, when cool, calm weather conditions and fewer predators contribute to favorable migratory conditions (Able 1973, Kerlinger 1995). Monitoring the nocturnal activities of migrants presents tremendous challenges to researchers because the migrating birds cannot be observed directly. Radar has been shown to be a useful tool for estimating the magnitude and directionality of migration events (e.g., Gauthreaux 1996), and there is a consistent relationship between radar analysis of nightly migration events and ground census data the following day (Zehnder and Karlsson 2001, Peckford and Taylor 2008). Radar data continue to provide significant information on avian nocturnal migration (e.g., Chilson et al. 2012), such as the responses of migratory animals to different weather conditions and major landscape influences, such as the Great Lakes (see Diehl et al. 2003). A major limitation of radar, however, is that species identity and flock composition cannot be discerned, which restricts the usefulness of radar data in population studies (Larkin et al. 2002).

Recording nocturnal flight calls is an understudied method of migration monitoring. Nocturnal flight calls are characteristically short, high-frequency, narrow-bandwidth vocalizations of 1–11 kHz (Farnsworth 2007, Evans and O'Brien 2002). Many migratory taxa produce night flight calls—including warblers, thrushes, and sparrows—and in many cases, these vocalizations are species distinctive (Evans and O'Brien 2002, Lanzone et al. 2009). Not all birds produce night flight calls, and although many woodpeckers, corvids, larks, swallows, and finches give flight calls regularly, they are diurnal migrants and rarely call at night (Farnsworth 2005). It has been suggested that several species of nocturnal migrants do not make flight calls at all, including New World flycatchers, vireos, and mimids (Farnsworth 2005). Although the functions of night flight calls are not well understood, they have been suggested to stimulate migratory restlessness (*Zugunruhe*), maintain flock contact during migration, and assist in orientation (Hamilton 1962, Farnsworth 2005). Recent radar research supports earlier anecdotal reports that birds move in much looser flocks during migration at night than in their daytime feeding behavior at stopover locations (Larkin and Szafoni 2008); flight calls may help orient individuals in these loose flocks.

Interest in analysis of night flight calls has grown over the past decade as technological developments have resulted in better recording and archiving techniques. However, identification of migrants on the basis of their flight calls alone continues to be a major challenge in this field (Graber and Cochran 1960, Lanzone et al. 2009). Spectrograms of some species' night flight calls often show very high similarity or exhibit extensive variability, making them difficult to distinguish from other species (Evans and Rosenberg 2000). Careful recordings and quantitative analyses of night flight calls, such as those of Evans and O'Brien (2002) and Lanzone et al. (2009), are required before we can confidently use this technique alongside existing migration monitoring strategies.

Here, we evaluate recordings of night flight calls as a tool for migration monitoring in a southern Great Lakes

ecosystem. We compare thousands of hours of nocturnal acoustic recordings with mist-net data from 2 migration monitoring stations in Ontario, Canada, focusing on the numbers of animals detected by acoustic recording versus mist netting. We also evaluate the seasonal timing of migration by comparing the median arrival dates of animals in the acoustic data versus mist-net data, as well as daily and weekly totals for 6 common migratory species with distinctive night flight calls. If recordings of night flight calls represent a compelling migration monitoring tool, we predicted that we would find a strong correspondence between acoustic data and mist-net data for both magnitude and timing of migration.

METHODS

General Field Methods and Study Location

We deployed 7 digital recorders during the 2012 spring migration (April 15–June 10) and fall migration (August 15–November 10). Three recording units were deployed on Pelee Island: 2 were placed 100 m apart at a bird-banding station located in Fish Point Provincial Nature Reserve (41°44′N, 82°40′W), and the third was deployed 15 km north, at Lighthouse Point Provincial Nature Reserve (41°47′N, 82°38′W) on the northern end of the island (Figure 1). Four recording units were deployed on the mainland, on the north shore of Lake Erie: 1 unit at a bird-banding station at Holiday Beach Conservation Area (42°02′N, 83°02′W); a second unit at a private woodlot near the town of McGregor, Ontario (42°06′N, 82°59′W; 11 km north-northeast of Holiday Beach); a third unit at Cedar Creek Conservation Area (41°00′N, 82°47′W; 21 km east of Holiday Beach); and a fourth within Point Pelee National Park (41°56′N, 82°30′W; 22 km east-southeast of Cedar Creek; Figure 1). These locations were selected because of their association with 2 long-standing migration monitoring stations (see detailed description below) and because they were in regional conservation areas with minimal ambient noise (anthropogenic noise, apart from airplanes, were rarely evident in our recordings) and artificial light (all microphones were positioned as far from anthropogenic light sources as possible). Without prominent artificial light at the recording locations, we assumed that we were counting true flyover migrants and not birds that were circling light sources or that had increased their calling rate in response to disorientation by light sources (Evans et al. 2007, Poot et al. 2008).

Acoustic Recordings

We used Wildlife Acoustics (Maynard, Massachusetts) USASM-2 Song Meter recorders at all 7 recording locations. Recordings were collected with 44,100-Hz sampling frequency with 16-bit accuracy in WAVE format in files that were 1 hr 59 min in length; we left a 1-min gap
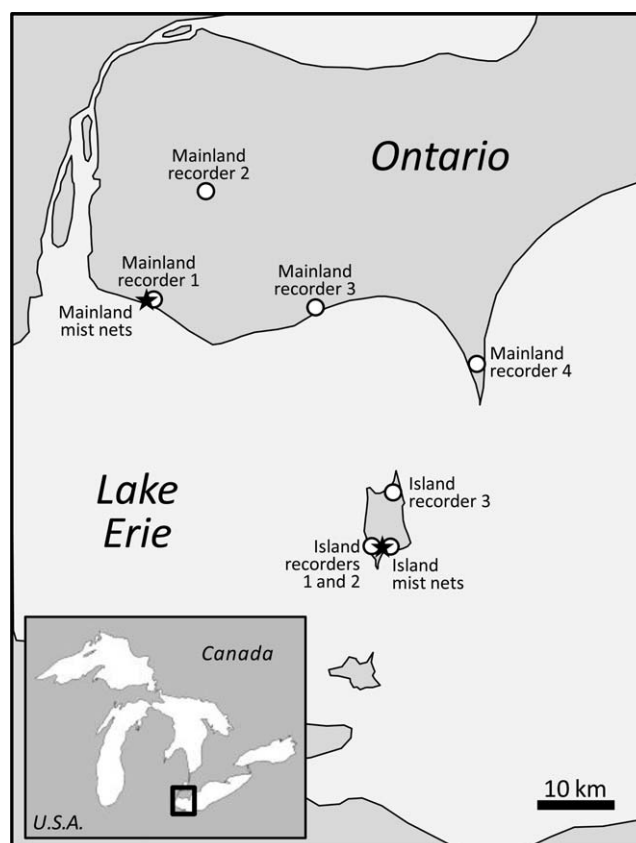

FIGURE 1. Map of the study area in Essex County in southwestern Ontario, Canada, showing the approximate locations of 7 automated acoustic recorders that collected flight calls of passing migrants at night (white circles) and of the 2 banding stations that sampled stopover migrants during the day (black stars).

between subsequent files to allow recorders to write the recordings to flash memory. This 1-min gap is not ideal, because our recordings will have missed any night flight calls for 1 min out of every 2 hr of recording, yet this was necessitated by the equipment; future updates to hardware should aim to eliminate this problem. We used omnidirectional microphones (Wildlife Acoustics SMX-NFC) mounted by the manufacturer at the center of a 30-cm^2 Plexiglas sound baffle to reduce interference from noise originating below the microphones. The detection range of these microphones has not been quantified, but other night-flight-call microphones have been suggested to record calls at distances of 250–500 m (Evans and Mellinger 1999, Larkin et al. 2002). We mounted microphones on top of a 5.8-m pole. Our objective at each site was to get the microphones above the tree canopy to reduce any interference noise from leaves, insects, and amphibians. In most locations, this was achieved by lashing the microphone pole to the side of a tree or a post. At both migration monitoring stations, we set up the

recorders in the immediate vicinity of the mist nets (at the island banding station, we set up 2 recorders 100 m apart at either end of the netting area; at the mainland banding station, we set up 1 recorder near the center of the netting area). All units were visited every 3 to 5 days to collect recordings and change batteries.

Following the Nocturnal Flight Call Count Protocol developed by eBird (see Acknowledgments), we programmed the Song Meters to record between the period of astronomical dusk and astronomical dawn, when the sun was lower than 18° below the horizon. We used data from the U.S. Naval Observatory website (see Acknowledgments) to determine these times for each of our recording locations. Given this recording window, we assumed that we avoided recording individuals that were calling from the ground shortly after dusk (a behavior associated with *Zugunruhe*; Farnsworth 2005) or near dawn (a behavior that may assist with habitat selection during descent or landscape relocation flights; Graber and Cochran 1960, Farnsworth 2005).

Analysis of Acoustic Recordings

We visualized recordings as sound spectrograms with Syrinx-PC sound analysis software (J. Burt, Seattle, Washington, USA). A team of 12 sound analysts scanned through the recordings, visualizing 30 s of recording at a time, within a frequency range of 0–11,000 Hz (spectral settings: 1,024 FFT size, Blackman window). Analysts used the cursors in Syrinx-PC to annotate the time and frequency coordinates of each night flight call. We attempted to use automated-detection software approaches to speed up this process; however, because of the high number of false detections from background noise (e.g., insects, wind, rain), we chose to scan through recordings manually to ensure the highest possible accuracy in detecting all sounds of interest (as recommended by Swiston and Mennill 2009). The first stage of analysis was completed when all hours of nocturnal recordings had been scanned and each night flight call had been annotated in Syrinx-PC. We scanned recordings from all 7 recorders on the same nights, regardless of noise due to wind and rain, so that we had an equal sampling period for each of our 7 recorders; we skipped nights when wind, rain, and insect noise made detection impossible.

In the second stage of our analysis, we examined all annotations and assigned each annotated sound to a particular species or group of species (see Supplemental Material Appendix S1). We visualized each sound that was annotated in the first stage of analysis in Syrinx-PC (spectral settings: 0.5 ms line^{-1}, 256 FFT size, Blackman window). Using an existing library of reference recordings, *Flight Calls of Migratory Birds: Eastern North American Landbirds* CD-ROM (Evans and O'Brien 2002), as well as other reference guides, including recordings and spectro-

grams from OldBird.org, XenoCanto, and Cornell Lab of Ornithology, we constructed a classification chart (Supplemental Material Appendix S1) modified from Evans and Rosenberg (2000). After comparing our own recorded flight calls to the reference libraries, we determined that 67 species of night migrants could be classified to the species level (i.e. their night flight calls were distinctive at the species level) or into 8 distinct bioacoustic categories (details of each category are provided in Supplemental Material Appendix S1). Some of these bioacoustic categories contained only 2 species (e.g., the category "FOSP/SOSP" included both Fox Sparrows [*Passerella iliaca*] and Song Sparrows [*Melospiza melodia*]), whereas other bioacoustic categories contained ≥9 species (e.g., the "*zeep*" category included many species of warbler; Supplemental Material Appendix S1). Several species with variable night flight calls spanned multiple bioacoustic categories or were classified as distinct at the species level as well as belonging to a broader category (see Supplemental Appendix S1); for example, Ovenbirds (*Seiurus aurocapilla*) produce a distinctive checkmark-shaped flight call that is species-specific but also produce calls that consist only of a frequency-modulated upsweep (i.e. the "up" complex). Hereafter, we refer to these bioacoustic categories as "species-groups," each comprising ≥2 species with flight calls that we could not readily distinguish. Any night flight calls that were quiet, distorted, or that did not match the reference library were classified as "unidentified."

Diurnal Migration Monitoring Data

We compared our bioacoustic data with mist-net data that were collected concurrently with the recordings by 2 migration monitoring stations. Both stations operate nets in similar habitats of semimature deciduous forest dominated by silver maple (*Acer saccharinum*) and red maple (*A. rubrum*), with eastern cottonwood (*Populus deltoides*), black ash (*Fraxinus nigra*), white elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), and pin oak (*Quercus palustris*).

The banding station on Pelee Island operated 10 mist nets and, as a member of the Canadian Migration Monitoring Network, followed the monitoring protocol recommendations of Hussell and Ralph (2005). During the spring of 2012, they captured birds from April 15 to June 10; during the fall of 2012, they captured birds from August 15 to November 10. The nets at this station were open half an hour before sunrise and operated for 6 hr, excluding downtime when nets were closed because of either inclement weather (rain or wind) or high bird volume (when too many birds were captured to process safely). The banding station on the mainland (Holiday Beach Migration Observatory) operated ≤16 nets during the fall migration (August 13–November 11) but did not

capture birds at this location during the spring. As a volunteer banding station, this observatory varied its netting hours according to the availability of volunteers. In order to standardize the capture effort between the 2 banding stations, we divided the number of birds captured in mist nets by the number of hours that the nets were operated.

To facilitate direct comparison between our acoustic data and the mist-net data, we assigned each captured bird to a category that corresponded to the bioacoustic categories presented in Supplemental Material Appendix S1. We pooled mist-net data for bird species whose night flight calls are indistinguishable (for details, see Supplemental Material Appendix S1). For example, all Fox Sparrows and Song Sparrows captured in mist nets were assigned to the "FOSP/SOSP" species-group of bird captures. This enabled us to make direct comparisons between the species and species-groups detected in the acoustic dataset and the mist-net dataset.

Statistical Analysis

To assess the similarity in the number of migrants detected by mist-net captures and nocturnal acoustic recordings, we tested for correlations between mist-net data and acoustic data. Our sample sizes for these analyses included all species or species-groups that we detected in either the mist-net or acoustic datasets within each season: $n = 39$ in fall (the 40 bioacoustic categories indicated in Supplemental Material Appendix S1 except for cuckoos, which were not detected by either method in fall) and $n = 37$ in spring. Dickcissels (*Spiza americana*), Golden-crowned Kinglets (*Regulus satrapa*), and Pine Siskins (*Spinus pinus*) were not detected by either method in spring.

To determine whether mist-net data and acoustic data produced similar information on the timing of passage, we ranked all mist-net detections and acoustic detections by ordinal date for each species or species-group (separate analyses for spring and fall). We then calculated the date at which 10%, 50%, and 90% of detections occurred for each species or species-group for each technique. Our sample size for these analyses included all species or species-groups for which we had ≥5 detections in both the mist-net and the acoustic datasets. To evaluate whether the correspondence between mist-net data and acoustic data varied over the course of the season, we plotted a line of perfect correspondence in our scatterplots of median arrival dates and calculated the residuals to this line; we then tested for correlations between these residuals and date.

For our analyses of both the magnitude and the timing of migration, we compared acoustic data from mainland recorder 1 with the mainland net data, and data from island recorders 1 and 2 with the island net data (see Figure 1), as well as the data from all recorders pooled. We

did this because we were interested in comparing acoustic with mist-net data at a local scale (i.e. 1 microphone placed very near to the mist nets), as well as at a regional scale (i.e. all 7 microphones in a broader geographic area).

We conducted additional analyses of the timing of migration for 6 focal species, focusing on species with distinctive night flight calls that were present in both the mist-net dataset and the acoustic dataset in ample numbers: Swainson's Thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*C. minimus*), American Redstart (*Setophaga ruticilla*), Black-throated Blue Warbler (*S. caerulescens*), Ovenbird, and White-throated Sparrow (*Zonotrichia albicollis*). For each of these 6 species, we compared the number of birds captured in mist nets during the day with the number of detections in our recordings from the previous night. Given that daily counts can be highly variable (Graber and Cochran 1960), we also compared the number of birds captured in mist nets and the number of acoustic detections on a weekly basis. For both the daily and weekly analyses, we restricted our analysis to the period between the first and last detection of each of the species within each season.

We conducted our analyses in JMP version 10 (SAS Institute, Cary, North Carolina, USA). When both the banding data and acoustic data were normally distributed, or normalized by log transformation, we used Pearson correlations, and we report Pearson correlation coefficients (r); otherwise, we used Spearman rank correlations, and we report Spearman correlation coefficients (ρ). All statistical tests are two-tailed. All statistics are presented as means ± SE.

RESULTS

At the 7 recording stations, we collected 2,157 hr of nocturnal recordings over 58 nights during the spring migration and 4,080 hr over 63 nights during the fall migration, for a total of 6,237 hr of recordings over the year. Within these recordings, we annotated 60,013 nocturnal flight calls: 22,554 during the spring migration (10.5 calls hr^{-1}) and 37,459 during the fall migration (9.2 calls hr^{-1}). We were able to classify with confidence 45,775 (76%) of the calls into 40 bioacoustic categories (see Supplemental Material Appendix S1).

On Pelee Island, 834 birds of 62 species were captured during spring migration and 2,079 birds of 75 species were captured during fall migration. On the mainland at Holiday Beach Conservation Area, 2,711 migrants of 63 species were captured during the fall migration. Some birds, such as flycatchers and vireos, were detected only in the banding data; other birds, such as cuckoos (*Coccyzus* spp.), White-crowned Sparrows (*Z. leucophrys*), and Chipping Sparrows (*Spizella passerina*), were detected only in our acoustic data.
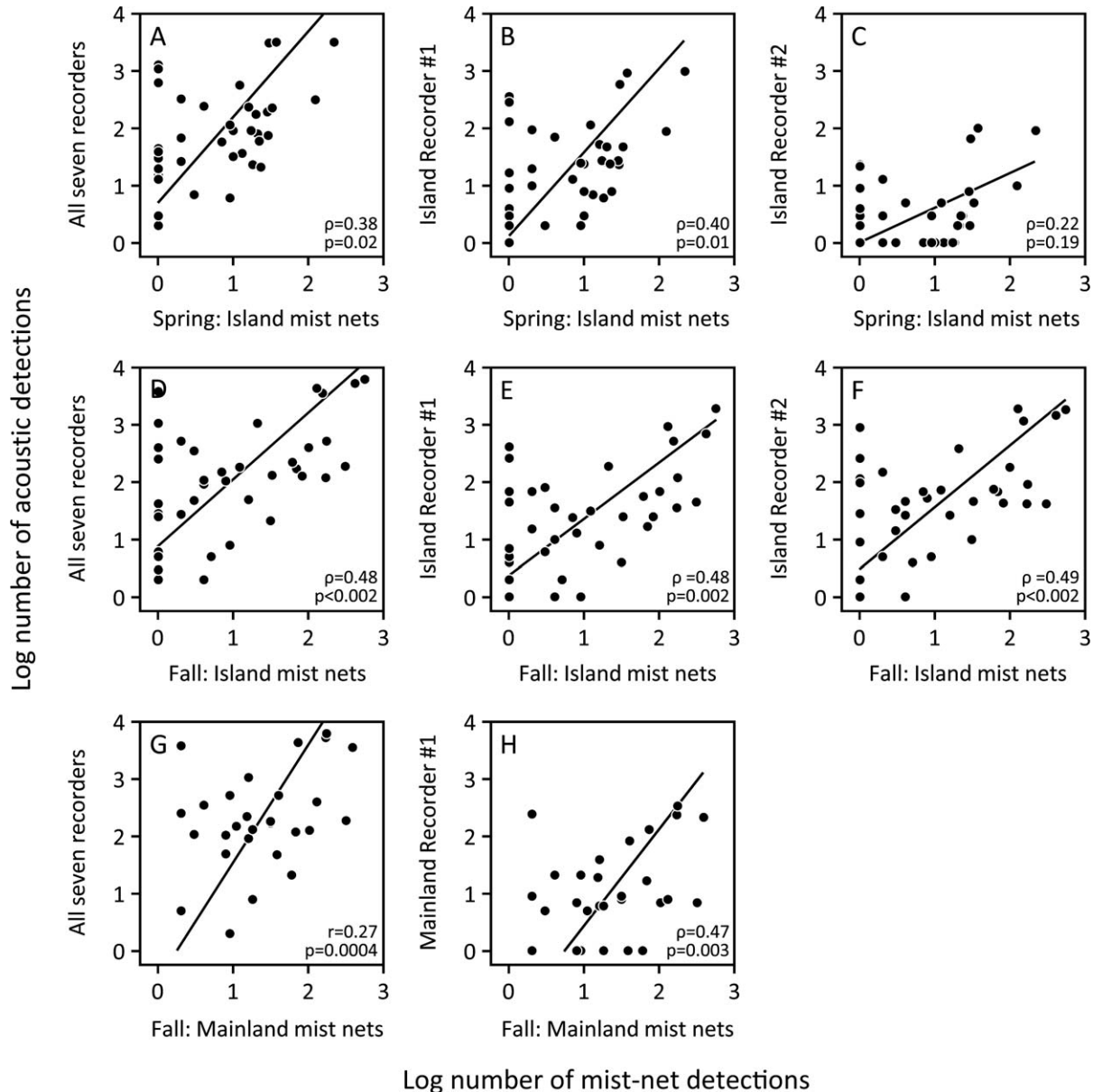
FIGURE 2. Scatterplots of the numbers of migratory birds detected by acoustic recordings reveal positive correlations with the numbers of birds detected by captures in mist nets. Each data point represents the log-transformed number of detections of a species or species-group ($n = 37$ in spring; $n = 39$ in fall). Lines show the principal axes to highlight the trends in the data. Three analyses are shown for spring: (**A**) acoustic data from all 7 recorders vs. island net data; (**B**) acoustic data from island recorder 1 vs. island net data; and (**C**) acoustic data from island recorder 2 vs. island net data. Five analyses are shown for fall: (**D**) acoustic data from all 7 recorders vs. island net data; (**E**) acoustic data from island recorder 1 vs. island net data; (**F**) acoustic data from island recorder 2 vs. island net data; (**G**) acoustic data from all 7 recorders vs. mainland net data; and (**H**) acoustic data from mainland recorder 1 vs. mainland net data.

Magnitude of Migration

During both spring and fall migration, the number of migratory birds detected by acoustic monitoring showed a positive correlation with the number detected in mist nets (Figure 2). This pattern held true when we compared mist-net data with the pooled acoustic data from all 7 recorders (Figure 2A, 2D, 2G) or to the acoustic data from only the

recorder closest to the mist nets (Figure 2B, 2C, 2E, 2F, 2H; $n = 37$ species or species-groups in spring; $n = 39$ species or species-groups in fall).

Seasonal Timing of Migration

To evaluate whether acoustic monitoring provides reliable information on the seasonal timing of migration, we
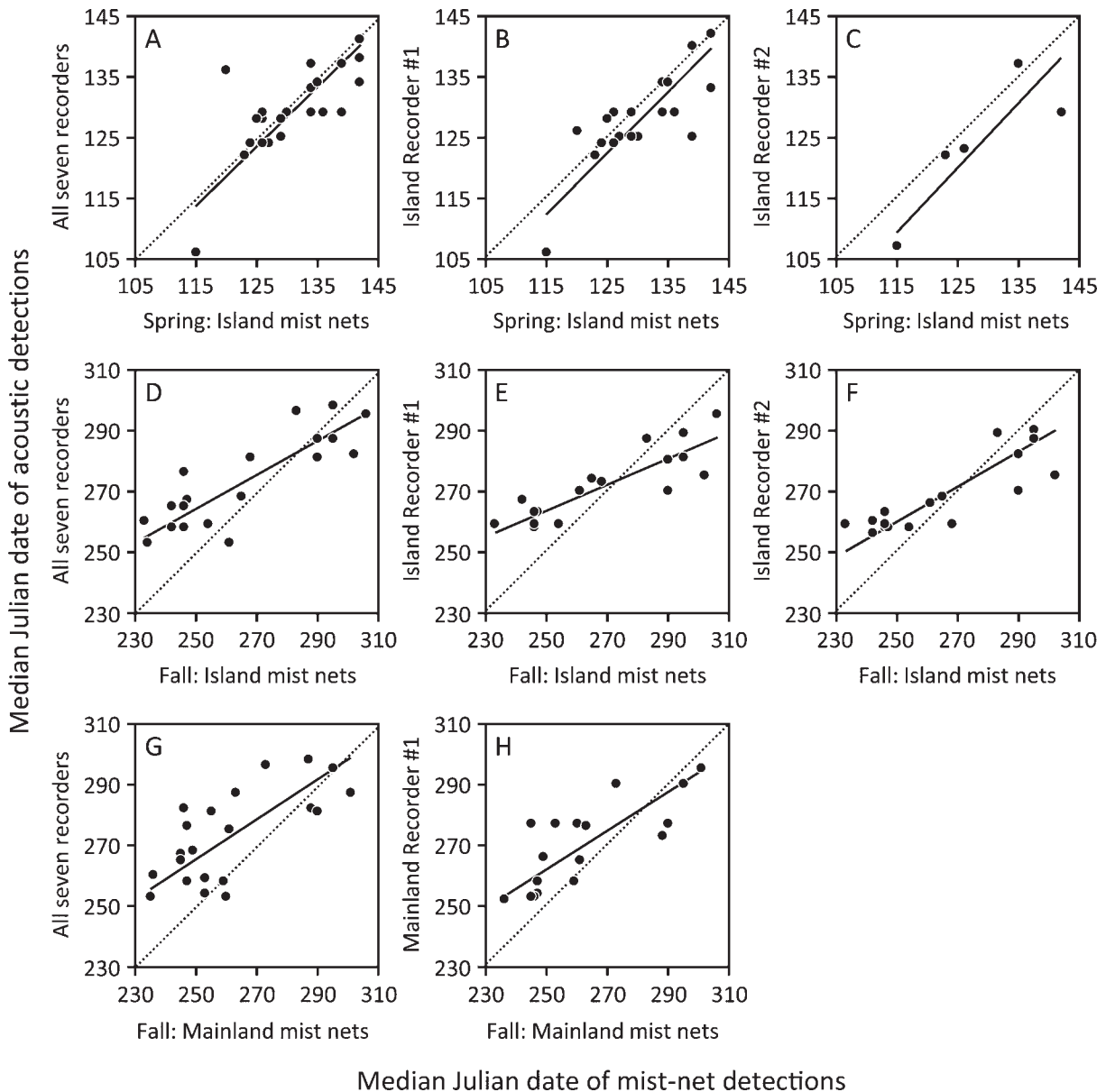
FIGURE 3. Scatterplots of the median dates of passage of migratory birds detected by acoustic recordings reveal positive correlations with the median dates of passage of birds detected by captures in mist nets. Each data point represents the median ordinal date for all detections within a season for each species or species group. Solid lines show the principal axes to highlight trends in the data; dotted lines show lines of perfect concordance, for reference. Three analyses are shown for spring data: (**A**) acoustic data from all 7 recorders vs. island net data; (**B**) acoustic data from island recorder 1 vs. island net data; and (**C**) acoustic data from island recorder 2 vs. island net data. Five analyses are shown for fall data: (**D**) acoustic data from all 7 recorders vs. island net data; (**E**) acoustic data from island recorder 1 vs. island net data; (**F**) acoustic data from island recorder 2 vs. island net data; (**G**) acoustic data from all 7 recorders vs. mainland net data; and (**H**) acoustic data from mainland recorder 1 vs. mainland net data. Statistical details are given in Table 1.

compared the median arrival date for all species or species-groups for which we had ≥ 5 detections in both the acoustic and mist-net datasets. We found positive correlations in median arrival date between acoustic data and mist-net data (Figure 3 and Table 1). The positive relationship held true when we compared mist-net data

with the pooled acoustic data from all of our recorders (i.e. Figure 3A, 3D, 3G), as well as when we compared the acoustic data from only the local microphone near the mist nets (i.e. Figure 3B, 3C, 3E, 3F, 3H). Similarly, we found significant positive correlations among the passage dates for the 10th and 90th percentiles of the total detected

TABLE 1. Comparison of the timing of migration as assessed through mist-net data and night-flight-call acoustic data ($n =$ number of species or species-groups for which there were ≥ 5 detections in both the mist-net and acoustic datasets). Detections of night flight calls show significant correlations for the timing of the 10th, 50th, and 90th percentiles of passage migrants in spring and fall in comparison to mist-net data.

Season	Net data	Acoustic data	Comparison of 10th percentile			Comparison of 50th percentile			Comparison of 90th percentile		
			r	P	n	r	P	n	r	P	n
Spring	Island	All recorders	0.48	0.01	25	0.67	0.002	25	0.54	0.006	25
Spring	Island	Island recorder 1	0.71	0.0003	21	0.81	0.0001	21	0.75	0.0001	21
Spring	Island	Island recorder 2	0.79	0.06	6	0.83	0.04	6	0.79	0.06	6
Fall	Island	All recorders	0.61	0.006	19	0.86	0.0001	19	0.80	0.0001	19
Fall	Island	Island recorder 1	0.88	0.0001	17	0.84	0.0001	17	0.77	0.0003	17
Fall	Island	Island recorder 2	0.85	0.0001	18	0.86	0.0001	19	0.86	0.0001	18
Fall	Mainland	All recorders	0.45	0.04	21	0.71	0.0003	21	0.80	0.0001	21
Fall	Mainland	Mainland recorder 1	0.91	0.0001	16	0.76	0.0006	16	0.78	0.0003	16

population of each category of birds between the mist-net data and acoustic data (Table 1).

To evaluate whether the relationship between median arrival date in acoustic versus mist-net detections changed across the season, we plotted lines of perfect correspondence between the mist-net and acoustic datasets (Figure 3) and calculated residuals to this line. In spring, there was no correlation between date and these residual values ($r \leq -0.39$, $P \geq 0.08$ for data shown in Figure 3A–3C). In fall, however, residual values decreased significantly as the season progressed, both for our island comparisons ($r \geq -0.48$, $P \leq 0.04$ for data shown in Figure 3D–3F) and for our mainland comparisons ($r \geq -0.70$, $P \leq 0.004$ for data shown in Figure 3G, 3H); species with early median arrival dates showed greater lags between the median date of acoustic detection in relation to the median date of mist-net detection, and these lags decreased as the fall migration progressed.

Weekly and Daily Comparisons of Migration Timing

To further evaluate whether acoustic monitoring provides reliable information on migration timing, we compared bioacoustic and mist-net data for 6 focal species that produce species-distinctive night flight calls and that were present in both the acoustic and mist-net datasets in ample numbers: Swainson's Thrush, Gray-cheeked Thrush, Black-throated Blue Warbler, American Redstart, Oven-bird, and White-throated Sparrow. Comparisons of weekly totals showed that peaks in migration were coincident for all 6 species in spring (Figure 4). During fall migration, however, the peak in acoustic detections lagged after the peak in mist-net detections by ≥ 1 wk (Figure 4). Comparisons of daily totals showed considerable variation in the number of animals detected in mist nets and recordings on a daily basis (Figure 5), yet the number of detections showed significant positive correlations for both spring and fall data (Table 2).

Comparison between 2 Nearby Recorders

Two of our acoustic monitoring stations on Pelee Island were separated by only 100 m, allowing us to evaluate the similarity in data between nearby recorders. Surprisingly, during spring migration, 1 recorder detected >6 times as many calls as the other (5,296 vs. 853 detections). The pattern was reversed in the fall, with the other recorder detecting almost twice as many calls (6,927 vs. 11,428 detections, respectively). Despite these substantial differences in number of detections by the 2 nearby recorders, both acoustic datasets still showed a positive correlation with the magnitude-of-migration data (Figure 2) and the date-of-passage mist-net data (Figure 3 and Table 1).

DISCUSSION

Acoustic monitoring of night flight calls yields accurate information on both the number of migrants and the timing of their migration through a southern Great Lakes ecosystem. The tens of thousands of night flight calls we recorded during the spring and fall migrations matched our reference dataset, which included thousands of mist-net records from 2 migration monitoring stations. We found a close correspondence between the numbers of animals detected with acoustic monitoring and with mist nets, as well as the timing of their migration at both a daily and a weekly timescale. We conclude that acoustic recordings of night flight calls can provide a compelling migration monitoring strategy.

Previous studies have highlighted the effectiveness of monitoring night flight calls through comparison to radar data and diurnal survey data. Both Farnsworth et al. (2004) and Gagnon et al. (2010) found positive associations between Doppler radar reflectivity density and acoustic detections on a nightly basis, although both studies stressed the variability of this relationship. Unpublished investigations by J. Murray (2004) and R. L. Holberton et
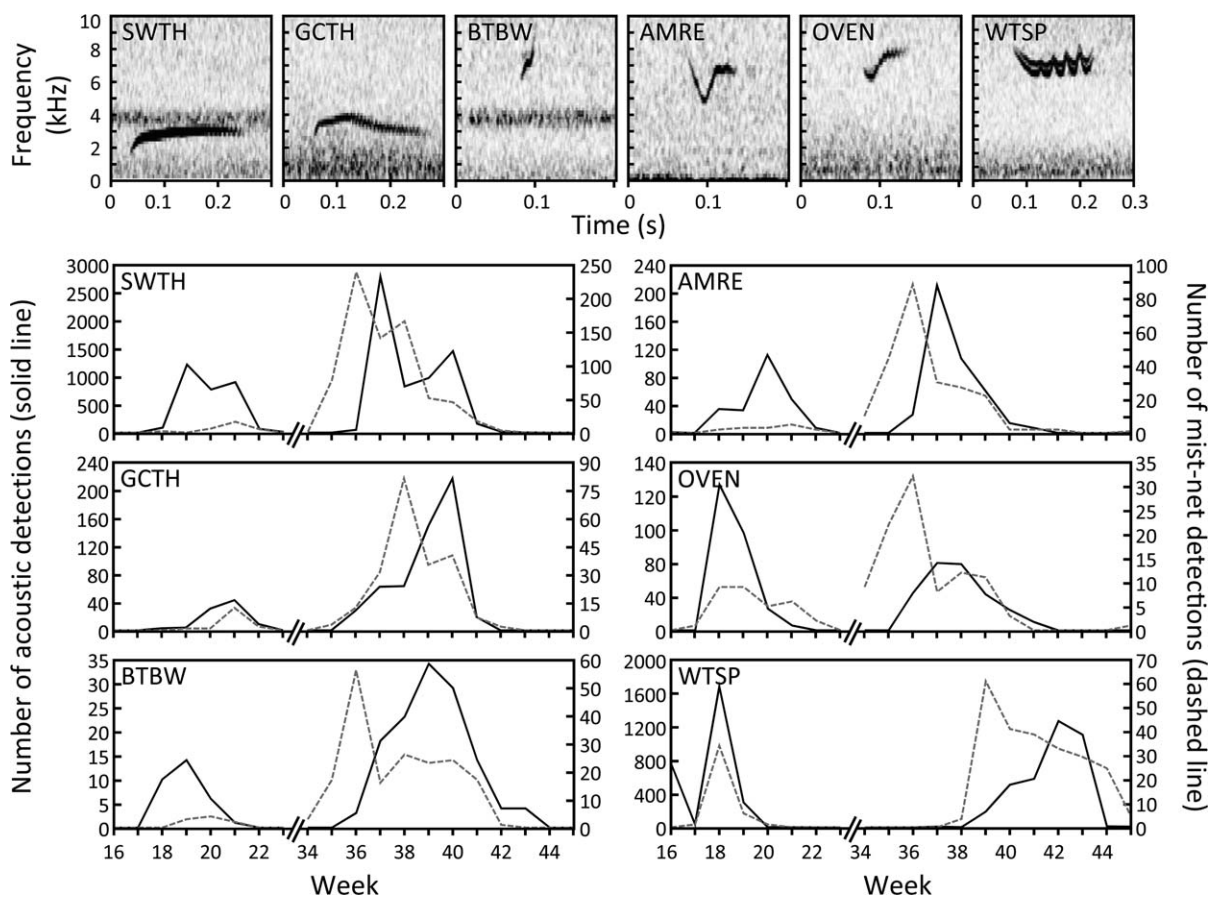
FIGURE 4. Sound spectrograms of the night flight calls of 6 migratory bird species (top) and plots of the weekly totals of acoustic detections (solid lines) and mist-net detections (dashed lines) during spring and fall migration of the 6 species: Swainson's Thrush (SWTH); Gray-cheeked Thrush (GCTH); Black-throated Blue Warbler (BTBW); American Redstart (AMRE); Ovenbird (OVEN); and White-throated Sparrow (WTSP). Data are shown for 8 wk of spring migration (week 16 is April 15–21, 2012) and 12 wk of fall migration (week 34 is August 19–25, 2012). Peaks of detection coincided in spring (weeks 16–23), whereas peaks of detection were earlier for net data than acoustic data in fall (weeks 34–45). Data from the island and mainland sites are pooled.

al. (2012) also support the reliability of night-flight-call data; these studies have shown that night-flight-call analysis can reflect diurnal counts of migratory birds.

In our study, acoustic detections of night flight calls provided similar insight on the timing of migration in comparison with mist-net records. We found strong correlations between the passage dates of the 10th, 50th, and 90th percentiles of the birds that flew over our recorders and those that were captured in mist nets. Therefore, these methods produce comparable insight on the timing of the migration in both spring and fall. Understanding seasonal variation in passage schedules for migrants has become an important topic in migration studies, particularly in response to emerging environmental influences such as climate change (Francis et al. 2009). Acoustic monitoring could enable us to recognize changes to migration timing, or changes in migratory routes, at a scale that is beyond the scope of traditional migration monitoring techniques.

In addition to our comparison across all species, we examined the timing of migration in 6 focal species chosen because of their distinctive night flight calls and their abundance within our acoustic and banding datasets. At a daily timescale, we found significant correlations between the number of migrants detected in our nocturnal recordings and the number of birds captured in mist nets the following morning, in both the spring and the fall, for all 6 focal species. Previous radar-based studies of Dickcissels by Larkin et al. (2002) also found a high correlation between radar and acoustic detections on a nightly basis.

At a weekly timescale, we found that the peak in acoustic and mist-net detections coincided during spring migration. During fall migration, our data suggest a lag of one to several weeks in the peak of acoustic detections after the peak in mist-net detections for all 6 focal species (Figure 4), and a similar lag in the median arrival date for species or species-groups that depart early in the fall
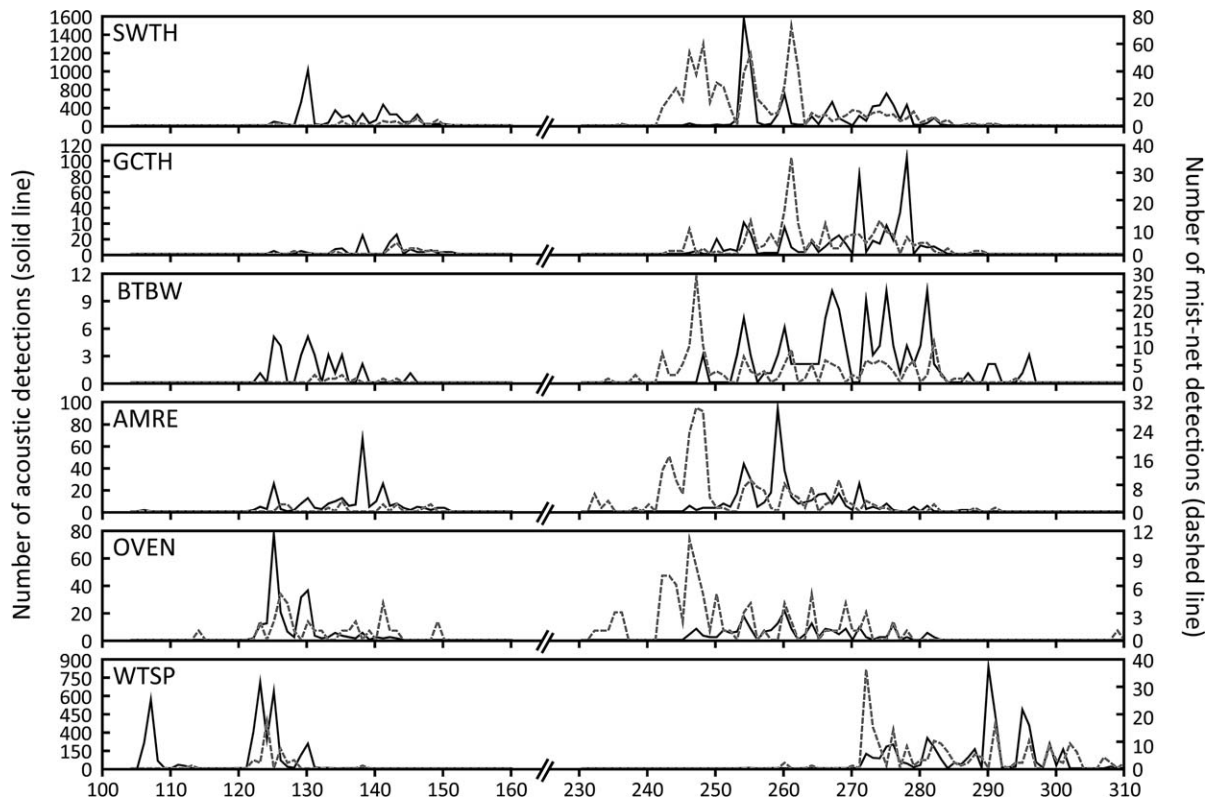
FIGURE 5. Plots of the daily totals of acoustic detections (solid lines) and mist-net detections (dashed lines) during spring and fall migration of 6 species: Swainson's Thrush (SWTH); Gray-cheeked Thrush (GCTH); Black-throated Blue Warbler (BTBW); American Redstart (AMRE); Ovenbird (OVEN); and White-throated Sparrow (WTSP). Data are shown for 8 wk of spring migration (ordinal date 100 is April 9, 2012) and 12 wk of fall migration (ordinal date 230 is August 17, 2012). Data from the island and mainland sites are pooled.

migration (Figure 3). The reason for this lag is unknown, but several explanations are possible. (1) This lag may reflect seasonal variation in the timing of migration between young and old birds. Hatch-year birds migrate at different times than adults in some species (Woodrey and Chandler 1997, Carlisle et al. 2005), and young birds may produce more night flight calls in migration (Farnsworth 2005), possibly because they are more easily disoriented (Gauthreaux 1982). Our mist-net data, however, suggest that this does not apply to our dataset; hatch-

year birds (HY) were captured significantly later than after-hatch-year birds (AHY) for only 1 of our 6 focal species (White-throated Sparrows; average $\pm$ SE ordinal date of capture: HY: 284.3 ± 0.9, AHY: 278.0 ± 1.7; t-test: $t = 3.3$, $P = 0.001$, $n = 200$), whereas hatch-year birds were captured significantly earlier for 1 species (American Redstart; HY: 249.6 ± 0.9, AHY: 252.9 ± 1.4; $t = 2.0$, $P = 0.05$, $n = 228$), and at similar times for the remaining 4 species ($t < 1.9$, $P > 0.06$, $n > 124$). (2) A second possibility is that the early mist-net captures represented

TABLE 2. Correlations between the number of migrants captured in mist nets and the number detected by nocturnal recordings for 6 common migratory species with distinctive night flight calls, calculated on a daily basis during spring and fall migration ($n =$ number of days compared between the first and last detection of each species within each season).

Species	Spring migration			Fall migration		
	ρ	P	n	ρ	P	n
Swainson's Thrush	0.56	0.0001	53	0.36	0.005	62
Gray-cheeked Thrush	0.46	0.02	27	0.41	0.004	47
American Redstart	0.24	0.11	45	0.45	0.0001	84
Black-throated Blue Warbler	0.13	0.55	23	0.32	0.01	63
Ovenbird	0.44	0.007	36	0.49	0.0001	78
White-throated Sparrow	0.31	0.05	41	0.51	0.0001	62

birds that bred in the local area and were then captured in the mist nets before migration began in earnest. This idea could explain the lag for 2 of the 6 focal species (American Redstart and Ovenbird), but the remaining 4 do not breed locally in our recording area (both species of thrush, Black-throated Blue Warbler, and White-throated Sparrow). (3) Finally, the lag in peak migratory activity could have been influenced by the masking influence of background noise in our early-fall recordings. For example, analysis of the first 2 wk of fall recordings (August 15–30, 2012) proved to be very difficult, owing to loud insect noise obscuring flight calls. This explanation cannot account for the similar lag we detected in White-throated Sparrows and Gray-cheeked Thrushes later in the fall migration, after insect noise had declined. Further investigations on migration and night-flight-call patterns of juvenile versus adult birds, and technical solutions that minimize the influence of noise on monitoring of night flight calls, will help distinguish between these biological and technical explanations.

We were surprised to find substantially different numbers of night flight calls detected by the 2 recorders on Pelee Island that were separated by only 100 m. In spring migration, 1 recorder detected >6 times as many calls as the other; in fall migration, the other recorder detected almost twice as many calls. We examined the recordings and the recording equipment and confirmed that these differences were not the result of any technical differences between the 2 sets of recordings. In spite of the differences in numbers detected by the 2 nearby recorders, both acoustic datasets still showed a positive correlation with the data on dates of passage and the magnitude of migration. Further investigation into the transmission properties of flight calls and the detection range of night-flight-call microphones will provide insight into how much airspace is sampled by each night-flight-call microphone. The differences we detected between the 2 nearby recorders suggest that detection rates and sampling efforts are highly localized. Furthermore, we found significant positive relationships in both the magnitude and the timing of migration, using the pooled acoustic data from all 7 microphones in our study area compared with the mist-net data from each station, but the relationships became even stronger when we used only the data from the microphones placed adjacent to the nets (Figures 2 and 3 and Table 1). This further suggests that migration patterns are localized on a relatively small geographic scale. These results suggest that future efforts will benefit from using multiple microphones at nearby locations rather than a single microphone at a single location, or by comparing data from multiple nearby recording locations and abandoning locations that have low numbers.

Historically, techniques for monitoring migratory birds have included daily visual counts and mist netting at stopover locations, and radar (reviewed by Milliken 2005, Dunn 2005). More recently, radio tracking has been useful for studying stopover and departure times of individual birds (e.g., Schmaljohann and Naef-Daenzer 2011, Mitchell et al. 2012), and geolocators have been instrumental in understanding individual migratory routes of larger passerines (e.g., Bairlein et al. 2012, Stanley et al. 2012). One limitation of mist netting as a migration monitoring strategy is that the number of migrants captured during one morning at a migration station is relatively small and may not necessarily represent the magnitude of the nocturnal migration from the previous night; opportune weather conditions might result in many birds passing over the netting area and, therefore, not being sampled by the nets. Additionally, differences in vegetation at banding stations, or habitat succession at banding stations, can bias trends in annual counts or mask possible changes in migratory routes (Francis et al. 2009). Acoustic monitoring does not suffer these shortcomings. For example, we recorded thousands of calls from Chipping Sparrows, Savannah Sparrows, and Field Sparrows—all open-habitat specialists—but these species were seldom or never captured in the mist nets, probably owing to the placement of nets in young forests. The acoustic data we collected suggest that 2 migration monitoring stations severely underestimate the number of Chipping, Savannah, and Field sparrows that pass though the region, which is likely also the case for other grassland species such as the Bobolink (*Dolichonyx oryzivorus*) and White-crowned Sparrow. Therefore, acoustic sampling can play a role in monitoring the timing of migration across a much wider geographic area than migration banding stations alone and may eliminate biases imposed by the habitat where mist nets are located.

Across many different taxa, passive acoustic monitoring has been used to determine presence–absence and to estimate group sizes, particularly in marine or nocturnal animals that are challenging to monitor using visual surveys alone (see Vaughan et al. 1997, Wang et al. 2005, Mellinger et al. 2007). As a migration monitoring technique, night-flight-call recording has numerous advantages for studying birds: (1) It facilitates the identification of species or species-groups during active flight; (2) it can be conducted in remote locations or difficult-to-access areas when banding or visual surveys are not feasible; (3) it samples birds while they are aloft, minimizing the effects of habitat on which species are detected; (4) it samples a much larger number of birds than mist netting or individual tracking; and (5) it is relatively accessible to birdwatchers and the public, requiring less training than mist netting and no permits. For these reasons, acoustic monitoring can play an important role in characterizing spring and fall global flyways.

One drawback of a solely acoustic approach to migration monitoring is that we may never be able to further separate some acoustically similar species from the larger species-groups. For example, the spectrogram of the flight call of Lincoln's Sparrow (*M. lincolnii*) cannot be reliably differentiated from that of Swamp Sparrow (*M. georgiana*). Although this may restrict this technique's usefulness for some taxa (e.g., species in the "*zeep*" category and the "up" category), it should not diminish the usefulness of this technology as a tool for monitoring the seasonal movements of other species of migratory birds. A second limitation is that acoustic monitoring cannot detect all species. Flycatchers and vireos, for example, do not appear to produce flight calls (Farnsworth 2005) but are detected regularly through mist netting. A third limitation of night-flight-call monitoring is that the influence of weather is poorly understood. Weather variables may influence birds' propensity to call as well as their migration altitude (and, consequently, their detection probability by night-flight-call microphones; Farnsworth 2005). Variation in local weather conditions may have contributed to the variation in flight-call data between our recording sites in this study. An optimal approach may involve multiple techniques for migration monitoring to produce the most comprehensive understanding of bird movement on large and small landscape scales (Milliken 2005, Peckford and Taylor 2008, Porzig et al. 2011).

Our results demonstrate that acoustic monitoring of nocturnal migrants provides an accurate tool for estimating species composition and timing of migratory events, as well as the magnitude of migration, for species that produce night flight calls and use forested stopover habitats. On a broad geographic scale, recording the long-term trends in the timing of spring and fall migrations can give insight into impacts from overarching influences such as climate change, which can potentially have complex and varied effects on the annual life cycle of migratory birds (Jenni and Kéry 2003, Van Buskirk et al. 2009). On a local scale, acoustic monitoring can help gauge the potential impacts of human developments, such as wind turbines, on migratory birds. The data we present here underscore the importance of using multiple techniques to monitor migratory birds during these major life history events (Peckford and Taylor 2008). Additional exploration of night-flight-call monitoring as a technique for monitoring passage migrants will continue to provide significant information on migration corridors, population trends, and the seasonality of bird behavior.

ACKNOWLEDGMENTS

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