BIOACOUSTICS
https://doi.org/10.1080/09524622.2018.1509373

# Decoding the ‘zeep’ complex: quantitative analysis of interspecific variation in the nocturnal flight calls of nine wood warbler species (*Parulidae* spp.)

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**ABSTRACT**

The “zeep” complex consists of nine birds that produce nocturnal flight calls with similar acoustic features. Our inability to distinguish these calls inhibits the acoustic monitoring of these species. We test the hypothesis that flight calls of nine warblers in the “zeep” complex show sufficient acoustic differences to allow differentiation. We investigate divergence in these vocalizations by recording birds held for banding and collecting additional recordings from sound libraries. We used three approaches to compare calls between species: analysis of variance in acoustic properties, discriminant analysis of acoustic properties, and spectrographic cross-correlation. The first approach revealed five species that were different in one or more acoustic properties. The second approach revealed a level of assignment to the correct species (73%) that exceeded levels expected by chance (36%). The third approach revealed calls of seven species to be significantly more similar to conspecific calls than heterospecific calls. Our results suggest the calls of many members of the “zeep” complex exhibit species-specific differences in structure, which may allow differentiation of at least five “zeep” species based on call alone. We advocate for the combined use of these three approaches for the comparison of “zeep” calls in future flight call studies.

**ARTICLE HISTORY**
Received 22 March 2018
Accepted 21 July 2018

**KEYWORDS**
Acoustic monitoring; migration monitoring; night flight calls; nocturnal flight calls; nocturnal migration; zeep

## Introduction

Acoustic recording technologies provide biologists with powerful tools to study and monitor animal populations across remote geographic areas and extended periods of time (Blumstein et al. 2011). Several studies have revealed that an acoustic approach to wildlife monitoring allows rapid collection of reliable data on the occurrence and abundance of target species (Parker 1991; Celis-Murillo et al. 2009). To date, acoustic recordings have been used to collect information efficiently for populations of birds (e.g. Sanders and Mennill 2014a), anurans (e.g. Acevedo and Villanueva-Rivera 2006), mammals (e.g. André et al. 2011; Payne et al. 2003; Russo and Jones 2003) and insects (e.g. Penone et al. 2013). As bioacoustic technologies have improved and become more

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accessible, recent decades have seen growth in the applied use of nocturnal flight call recordings as a powerful tool for monitoring the populations and movements of migratory birds (Evans and Rosenberg 2000; Sanders and Mennill 2014b).

Nocturnal flight calls are short (50–300 ms) species-specific vocalizations produced by diverse bird species, including warblers (*Parulidae*), sparrows (*Emberizidae*), thrushes (*Catharus*) and rails (*Rallidae*). These vocalizations are produced by birds primarily in association with migratory behaviour (Evans and O'Brien 2002; Farnsworth 2005). Nocturnal flight calls may be used to facilitate flock cohesion and to stimulate migratory restlessness (Hamilton 1962), although the biological function of nocturnal flight calls remains uncertain and little-studied (Farnsworth 2005). The recording of these calls has proven to be a compelling method for sampling the timing and magnitude of the nocturnal movements of migratory birds (Evans and Rosenberg 2000; Larkin et al. 2002; Farnsworth et al. 2004; Sanders and Mennill 2014b; Horton et al. 2015a). While other approaches for monitoring migrants provide valuable information on movements of birds in active flight (most notably, radar; Diehl et al. 2003), acoustic monitoring is currently the only approach capable of identifying the species of nocturnally migrating birds (Horton et al. 2015b). Nocturnal flight call detections can therefore provide important insight into migratory behaviours of birds during their nocturnal movements.

The capacity to identify the species of nocturnally migrating birds is a major advantage of acoustic monitoring, yet there are several challenges associated with this technique. The primary challenge of processing nocturnal flight call recordings is the dearth of information concerning the degree of acoustic variation in birds' nocturnal flight calls (Lanzone et al. 2009). To date, there has been limited research conducted on acoustic variation within these calls, with only one study investigating intraspecific variation (Griffiths et al. 2016). Interspecific analyses of variation within the warbler family have revealed a lack of morphological constraints on the evolution of flight call properties but found evidence for phylogenetic effects acting on these vocalizations (Farnsworth and Lovette 2005, 2008). The nocturnal flight calls of many warblers exhibit species-specific differences in fine structure (Evans and O'Brien 2002; Farnsworth 2005) and yet there has been no careful quantitative research on acoustic differences between species that produce calls with similar spectro-temporal properties. Without accurate information on the amount of variation within and between nocturnal flight calls of different species, it is difficult to develop reliable approaches to identify acoustically similar calls to the species level.

There have been several attempts to develop methods for automated identification of flight calls (e.g. machine learning, Taylor 1995; Damoulas et al. 2010; spectrographic cross-correlation, Keen et al. 2014). Although automated identification techniques may eventually become an efficient alternative to human classification, automated techniques experience higher rates of false positives and false negatives than human experts, both for flight calls (Keen et al. 2014) and other types of animal sounds (Swiston and Mennill 2009). The scarcity of information concerning variation in nocturnal flight calls has limited the development of both automated and human classification approaches for species identification of flight calls with similar structure (e.g. Sanders and Mennill 2014b). As a result, previous investigators have categorized species with highly similar flight calls into bioacoustic catch-all groups (e.g. Evans and O'Brien 2002; Sanders and Mennill 2014b). The 'zeep' category is one such group, consisting of nine migratory wood-warbler species: Worm-eating Warbler, *Helmitheros vermivorum*; Louisiana Waterthrush, *Parkesia motacilla*; Connecticut Warbler, *Oporornis agilis*; Cerulean Warbler, *Setophaga cerulea*; Magnolia Warbler, *Setophaga magnolia*; Bay-breasted Warbler, *Setophaga castanea*; Blackburnian Warbler, *Setophaga fusca*; Yellow Warbler, *Setophaga petechia*; and Blackpoll Warbler, *Setophaga striata* (Evans and O'Brien 2002; Sanders and Mennill 2014b). (Other species produce calls considered similar in structure, and sometimes those species are included in the 'zeep' complex, such as the Northern Waterthrush in Evans and O'Brien 2002; but we have focused on the nine species listed here, as in Sanders and Mennill 2014b.) The inability to identify 'zeep' calls to the species level reliably reduces the utility of nocturnal flight calls detections for population monitoring. By developing a library of high-quality recordings of flight calls produced by individuals of each species, we may find that these species exhibit differences in calls that would allow future 'zeep' recordings to be classified to the species level.

In this study, we use bioacoustic approaches to explore interspecific differences in the nocturnal flight calls of nine warbler species within the 'zeep' bioacoustic category. We hypothesized that these nine species exhibit differences in the fine structural details of their nocturnal flight calls, which would allow reliable species-level classification based on flight calls alone. To test this hypothesis, we collected recordings of nocturnal flight calls produced by birds held for banding at migration monitoring sites in southern Ontario and we supplemented these with recordings from existing sound libraries. We used three spectrographic analysis techniques: analysis of variance in fine structural features of calls, discriminant analysis of fine structural measurements of calls and spectrographic cross-correlation to quantify acoustic differences between species. This is the first study to investigate which bioacoustic properties may allow reliable discrimination between the nocturnal flight calls of the nine species in the 'zeep' complex. The ability to differentiate the 'zeep' flight calls of nocturnally migrating birds based on the fine structure would considerably improve the capabilities of acoustic recording for studying the nocturnal behaviours of these nine warbler species, including species of conservation concern (e.g. Cerulean Warbler, Louisiana Waterthrush and Worm-eating Warbler).

## Methods

### General field methods

We collected recordings from birds held for banding at two bird observatories in southern Ontario, Canada: Long Point Bird Observatory (42.5829°N, −80.3985°W) and Holiday Beach Migration Observatory (42.0322°N, −83.0437°W). We recorded birds at Holiday Beach Migration Observatory between 15 August and 31 October 2015 and 2016 and Long Point Bird Observatory between 2 April and 3 June 2016 and 2017. Holiday Beach Migration Observatory is located within the Holiday Beach Conservation Area on the north shore of the western basin of Lake Erie. Holiday Beach, in combination with the adjacent Big Creek Conservation Area, is listed as an Important Bird Area due to high concentrations of diurnal raptors and migratory land birds during fall migration. Long Point Bird Observatory is located at the base of the Long Point peninsula on the northern shore of Lake Erie. The peninsula is a 40 km

**Table 1.** Total number of individuals per species included in comparisons of flight call properties across species. We included one call per bird in analyses to avoid potential pseudo-replication. Flight calls included in our analyses were from our recordings or from public sources of animal sounds: Xeno-Canto (www.Xeno-Canto.org) and the Flight calls of migratory birds: eastern North American land birds (CD-ROM).

| Species | Total number of individuals | Recorded birds | Recordings from Evans and O'Brien | Recordings from Xeno-Canto |
|---|---|---|---|---|
| Worm-eating Warbler | 11 | 0 | 6 | 5 |
| Louisiana Waterthrush | 8 | 0 | 2 | 6 |
| Connecticut Warbler | 7 | 0 | 4 | 3 |
| Cerulean Warbler | 4 | 0 | 3 | 1 |
| Magnolia Warbler | 60 | 60 | 0 | 0 |
| Bay-Breasted Warbler | 25 | 15 | 6 | 4 |
| Blackburnian Warbler | 17 | 7 | 7 | 3 |
| Yellow Warbler | 28 | 23 | 5 | 0 |
| Blackpoll Warbler | 18 | 10 | 5 | 3 |
| Total | 178 | 115 | 38 | 25 |

sand spit hosting a wide array of habitats, including woodlands and marshes, and serves as an important migratory staging and stopover location for many passerine and waterfowl species.

Our study species included nine wood warbler species in the ‘zeep’ species-group: Worm-eating Warbler, Louisiana Waterthrush, Connecticut Warbler, Cerulean Warbler, Magnolia Warbler, Bay-breasted Warbler, Blackburnian Warbler, Yellow Warbler and Blackpoll Warbler. We caught and recorded birds of five species while they were held for banding: Magnolia Warbler, Bay-breasted Warbler, Blackburnian Warbler, Yellow Warbler and Blackpoll Warbler. We recorded 690 birds, of which 115 individuals vocalized. In order to sample less-common and cryptic species (e.g. Worm-eating Warbler, Cerulean Warbler) and to facilitate inclusion of all nine species in our analysis, we also collected recordings from public sources of flight call recordings: Xeno-Canto (http://www.xeno-canto.org; 25 individuals) and the *Flight Calls of Migratory Birds: Eastern North American Landbirds* CD-ROM (Evans and O’Brien 2002; 38 individuals; Table 1). All recordings taken from public sources indicated the birds were identified through visual confirmation.

Birds were captured with mist nets as part of the standard migration monitoring procedure at the two banding observatories. We banded birds with United States Geological Survey (USGS) bands marked with unique nine digit numbers and we transferred birds to a separate building, on site, equipped with a darkened and sound-dampened recording booth (as in Lanzone et al. 2009). We placed birds into a cylindrical, cloth chamber suspended within the booth for recording. We positioned an omni-directional microphone (Sennheiser ME62/K6 microphone) and digital recorder (Marantz PMD670; settings: WAV format, 44.1 kHz sampling frequency, 16-bit accuracy) 30 cm below the chamber to record the birds’ vocalizations. Using a loudspeaker, we exposed birds to acoustic stimuli of recordings of nocturnal flight calls from congeneric individuals to induce calling. Acoustic stimuli consisted of sequences of calls taken from the *Flight Calls of Migratory Birds: Eastern North American Landbirds* CD-ROM (Evans and O’Brien 2002). We attempted to create acoustic stimuli using only conspecific calls because previous research suggested birds respond more frequently to conspecific calls than heterospecific calls (Morris et al. 2016), but for all recorded species it was necessary to use calls from closely-related species (congeneric species) due to the limited availability of recordings. Each stimulus began with 45 s of silence to allow the bird to acclimate to surroundings. This period of silence was followed by a series of congeneric flight calls presented at 5-s intervals for the remaining duration of the recording session. We recorded birds for up to 5 min and then read the birds’ band number into the microphone. We immediately released birds back to the area they were captured. If birds showed signs of distress during the banding process, or early stages of the recording process, we released them immediately without collecting a recording.

## *Spectrographic analysis*

In the laboratory, we visualized recorded calls by generating spectrograms with Syrinx-PC (J. Burt, Seattle, WA; spectral settings: 4 ms line$^{-1}$, 256 FFT size, Blackman window). We scanned through recordings and extracted all calls produced by each bird as a separate WAV file. The calls of live birds were easy to differentiate from our

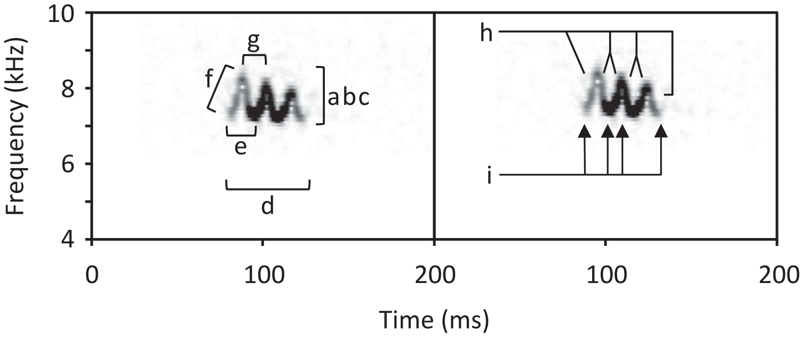

**Figure 1.** Sound spectrograms showing 14 acoustic measurements collected from nocturnal flight calls produced by migratory songbirds: (a) call bandwidth; (b) minimum frequency; (c) maximum frequency; (d) duration; (e) distance to maximum amplitude; (f) slope calculations of frequency modulations over time (start to end, minimum to maximum, and start to first frequency peak of the call); (g) inter-peak duration; (h) number of frequency modulations; (i) peak frequency at the start, maximum amplitude, centre, and end of the call.

playback stimuli due to the 5-s intervals between calls in our stimuli. To reduce background noise, we filtered the WAV files with a high pass filter at 4 kHz. We normalized the amplitude of the filtered calls to −1 dB in Adobe Audition (version 3.0; Adobe, San Jose, CA). We then measured the fine spectro-temporal parameters of each call using Avisoft-SAS (Avisoft Bioacoustics, Berlin, Germany; spectral settings: 0.73 ms line$^{-1}$, 256 FTT size, Blackman window). We assigned a sequential number to all calls recorded from each individual (ignoring calls where a portion of the signal was masked by background noise) and randomly selected one call from each individual, using a random number generator; we used this call in all subsequent measurements thereby avoiding pseudo-replication in our analyses.

For each call, we used AviSoft (Avisoft-SASLab Pro is Avisoft Bioacoustics, Berlin, Germany - Version 5.2.) to measure a total of 14 fine structural properties (Figure 1): bandwidth; minimum frequency; maximum frequency; duration; distance (time delay) from the start of the call to the point of maximum amplitude; number of frequency modulations; inter-peak duration; slope of frequency modulation from start to end of call; slope of frequency modulation from minimum to maximum frequencies; slope of frequency modulation from start to first peak of call; the peak frequency at multiple locations including the start, point-of-maximum-amplitude, centre and end.

We conducted spectrographic cross-correlation for 178 flight calls from the nine warbler species. We performed the cross-correlation in Avisoft SASLAB PRO correlator (Avisoft Bioacoustics, Berlin, Germany; 500 Hz maximum frequency deviation). Spectrographic cross-correlation compares each pair of sounds by overlaying spectrograms to provide a value between zero (no similarity in two spectrograms) and one (perfect similarity in two spectrograms; Cortopassi and Bradbury 2000).

### *Statistical analysis*

We used three statistical approaches to investigate differences in nocturnal flight call properties between nine warbler species. First, we used analysis of variance on the means of the 14 fine structural measurements and *post hoc* Tukey's tests to infer differences in flight call properties across species.

Second, we conducted a forward stepwise canonical discriminant analysis, with leave-one-out cross-validation, using 14 acoustic properties to determine whether flight calls can be assigned to species correctly based on spectral-temporal properties. We chose to apply canonical discriminant analysis rather than other classification methods (e.g. machine learning techniques) due to small sample size for multiple target species. Further, discriminant functions analysis has been shown to be effective at discerning subtle differences in the fine structure of bird calls (e.g. Baker and Logue 2003; Fitzsimmons et al. 2011). Our stepwise canonical discriminant analysis selected five variables for inclusion over five steps. At each step, we selected the variable that minimized the overall Wilks' Lambda score. Due to small sample sizes and to avoid violating the analytical assumptions of discriminant analyses, only six of the nine 'zeep' species were included in the canonical discriminant analysis of acoustic characteristics: Bay-breasted Warbler, Blackburnian Warbler, Blackpoll Warbler, Magnolia Warbler, Worm-eating Warbler and Yellow Warbler. Further, one Blackpoll Warbler call was unusually long and was classified as out-of-range and excluded, resulting in 159 flight calls for use in canonical discriminant analysis. Due to unequal sample sizes for each of the nine species, the number of calls included for each species influences the chance of any call being assigned to the correct species. As a result, we calculated the level of correct assignment by chance using the weighted mean of the probability of each call being classified to the correct species.

Third, we compared the mean within-species and between-species similarity scores for each bird, generated by spectrographic cross-correlation. We calculated the mean within-species and between-species scores for each individual and used a paired t-test or Wilcoxon matched-pairs signed-rank test to compare mean within and between scores for each species. If spectrographic cross-correlation revealed species-specificity in these calls, we expected mean similarity values to be higher when comparing calls within species versus between species.

If our hypothesis holds true, we predicted that one, two, or all three of these techniques would reveal differences between the species in the 'zeep' complex. All statistical analyses were conducted in SPSS, version 23 (Armonk, NY; IMB corp.).

## Results

### *Analysis of variance of flight call properties*

The nocturnal flight calls of the nine 'zeep' species all occupied a common acoustic space, sharing many spectral-temporal characteristics (Table 2; Figure 2), yet analysis of variance of each acoustic feature revealed significant test effects for all 14 acoustic measurements (Table 2). Three *post hoc* Tukey's tests revealed one species that was different from all the others, whereas the remaining *post hoc* comparisons did not, as summarized below.

**Table 2.** Means ± standard deviations of acoustic measurements of flight call properties for the nine ‘zeep’ warbler species. Bottom two rows show the results from analysis of variance of acoustic measurements and the sample sizes for each species are given in Table 1.

| Species | Duration (ms) | Distance to Max. Amplitude (ms) | Min. Freq. (kHz) | Max. Freq. (kHz) | Bandwidth (kHz) | Peak Freq. at Start (kHz) | Peak Freq. at End (kHz) | Peak Freq. at Centre (kHz) | Peak Freq. at Max. Amplitude (kHz) | Number of Freq. Modulations | Inter-peak Duration (ms) | Freq. Modulation: Start to End | Freq. Modulation: Min. to Max. | Freq. Modulation: Start to Peak |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Worm-eating Warbler | 46 ± 7 | 26 ± 3 | 7 ± 0.4 | 9 ± 0.4 | 1.9 ± 0.3 | 7.8 ± 0.6 | 7.9 ± 0.9 | 8.0 ± 0.6 | 8.0 ± 0.8 | 5.73 ± 1.7 | 12 ± 1 | −1 ± 18.2 | −43.5 ± 7.8 | −113 ± 187.9 |
| Louisiana Waterthrush | 77 ± 6 | 50 ± 2 | 7 ± 0.4 | 8.8 ± 0.3 | 1.8 ± 0.3 | 7.3 ± 0.1 | 7.3 ± 0.6 | 7.7 ± 0.6 | 7.6 ± 0.1 | 9.37 ± 2.3 | 15 ± 2 | −1 ± 8.1 | −23.6 ± 4.6 | −63.6 ± 78 |
| Connecticut Warbler | 43 ± 5 | 22 ± 3 | 6.8 ± 0.3 | 8.3 ± 0.4 | 1.5 ± 0.3 | 6.8 ± 0.3 | 7.5 ± 0.4 | 7.7 ± 0.7 | 7.3 ± 0.5 | 5.57 ± 1.3 | 13 ± 2 | −14.5 ± 8.1 | −36.4 ± 7.8 | −89.5 ± 79.4 |
| Cerulean Warbler | 50 ± 9 | 26 ± 6 | 6.3 ± 0.1 | 8 ± 0.4 | 1.7 ± 0.5 | 7.0 ± 0.6 | 6.9 ± 0.6 | 7.3 ± 0.7 | 6.7 ± 0.3 | 7.75 ± 1.3 | 14 ± 3 | 2 ± 9.9 | −35.1 ± 6.7 | −78.3 ± 200.8 |
| Magnolia Warbler | 43 ± 11 | 21 ± 10 | 6.7 ± 0.4 | 7.8 ± 0.6 | 1.1 ± 0.5 | 6.9 ± 0.5 | 7.0 ± 0.5 | 7.2 ± 0.4 | 7.0 ± 0.4 | 5.12 ± 1.6 | 14 ± 2 | −5 ± 13.6 | −28 ± 13.8 | −56.2 ± 46.6 |
| Bay-breasted Warbler | 46 ± 8 | 24 ± 9 | 6.7 ± 0.6 | 8 ± 0.6 | 1.2 ± 0.4 | 6.9 ± 0.5 | 7.2 ± 0.6 | 7.2 ± 0.6 | 7.2 ± 0.6 | 3.96 ± 0.9 | 23 ± 3 | −6.6 ± 10.9 | −29 ± 14.7 | −56.9 ± 29.3 |
| Blackburnian Warbler | 53 ± 20 | 25 ± 13 | 6.7 ± 0.5 | 8.7 ± 0.6 | 2 ± 0.6 | 6.8 ± 0.6 | 7.5 ± 0.9 | 7.7 ± 0.9 | 7.1 ± 0.6 | 5.35 ± 1.7 | 17 ± 2 | −16.3 ± 18.1 | −42.6 ± 14.3 | −144 ± 56.9 |
| Yellow Warbler | 47 ± 11 | 22 ± 7 | 5.9 ± 0.8 | 7.4 ± 0.8 | 1.5 ± 0.4 | 6.4 ± 0.8 | 6.3 ± 0.8 | 6.7 ± 0.8 | 6.5 ± 0.7 | 5.86 ± 2.1 | 14 ± 1 | 2.8 ± 14.9 | −34.1 ± 13.4 | −157.5 ± 74.9 |
| Blackpoll Warbler | 53 ± 7 | 25 ± 6 | 6.7 ± 0.4 | 8.1 ± 0.4 | 1.4 ± 0.4 | 6.9 ± 0.5 | 7.2 ± 0.3 | 7.3 ± 0.5 | 7.2 ± 0.5 | 6.56 ± 1.3 | 15 ± 1 | −7.2 ± 10.7 | −27.1 ± 7.2 | −127.1 ± 37.5 |
| *F* value | 10.53 | 11.25 | 8.07 | 13.44 | 10.67 | 7.01 | 9.69 | 8.03 | 10.96 | 10.06 | 34.11 | 3.43 | 4.71 | 6.99 |
| *p* Value | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | 0.001 | < 0.001 | < 0.001 |

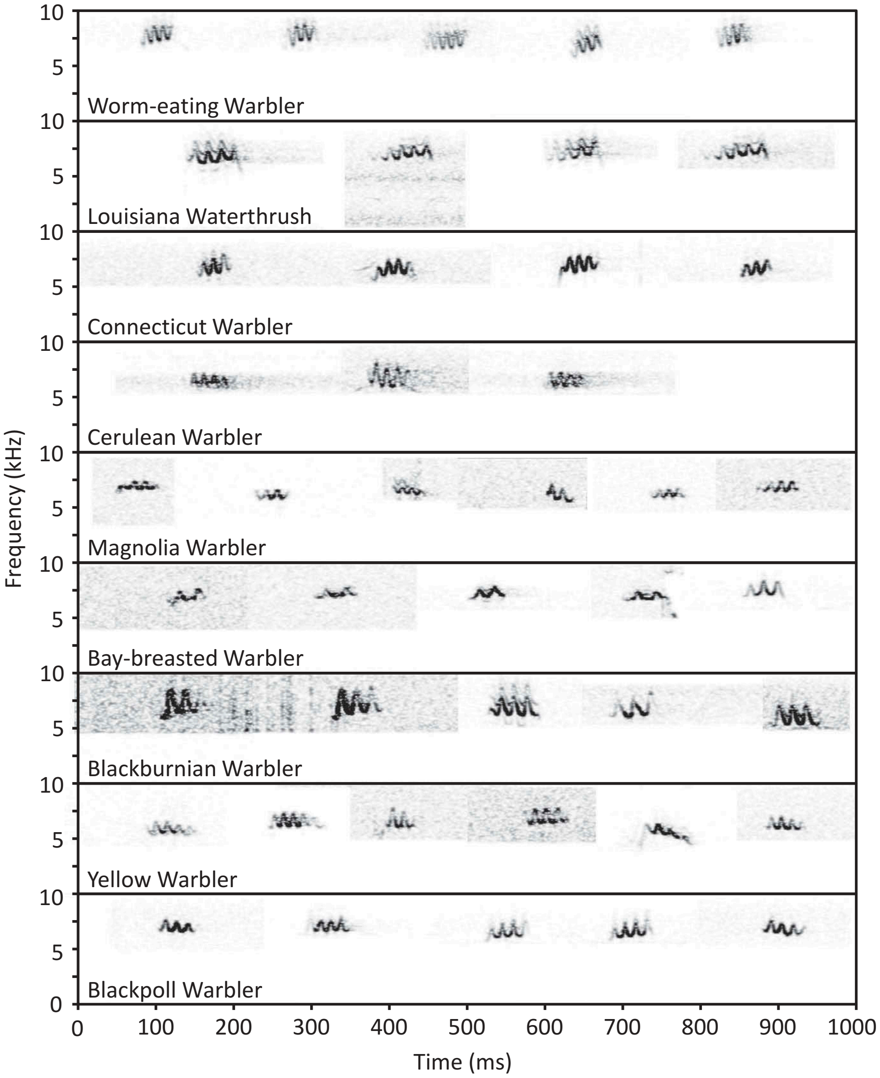

**Figure 2.** Sound spectrograms showing nocturnal flight calls produced by the nine warbler species in the 'zeep' species-group, a bioacoustic category of birds that produce similarly structured flight calls. Recordings of flight calls were recorded during spring and fall 2015–2017 migration periods and collected from public sources of animal sounds (e.g. Xeno-Canto and the Flight calls of migratory birds: eastern North American land birds CD-ROM).

The mean duration of flight calls showed significant variation between the nine 'zeep' species (ANOVA: $F_8 = 10.53$; $p \leq 0.001$): Louisiana Waterthrush flight calls were significantly longer in duration than all others (Figure 3(a); Tukey's *post hoc* test: $q = 3.14$; $p \leq 0.001$), whereas all eight remaining species' calls were similar in duration. The distance to maximum amplitude also showed significant variation between species (ANOVA: $F_8 = 11.24$; $p \leq 0.001$): Louisiana Waterthrush calls had a significantly longer distance from the start of the call to the point of maximum amplitude in comparison to

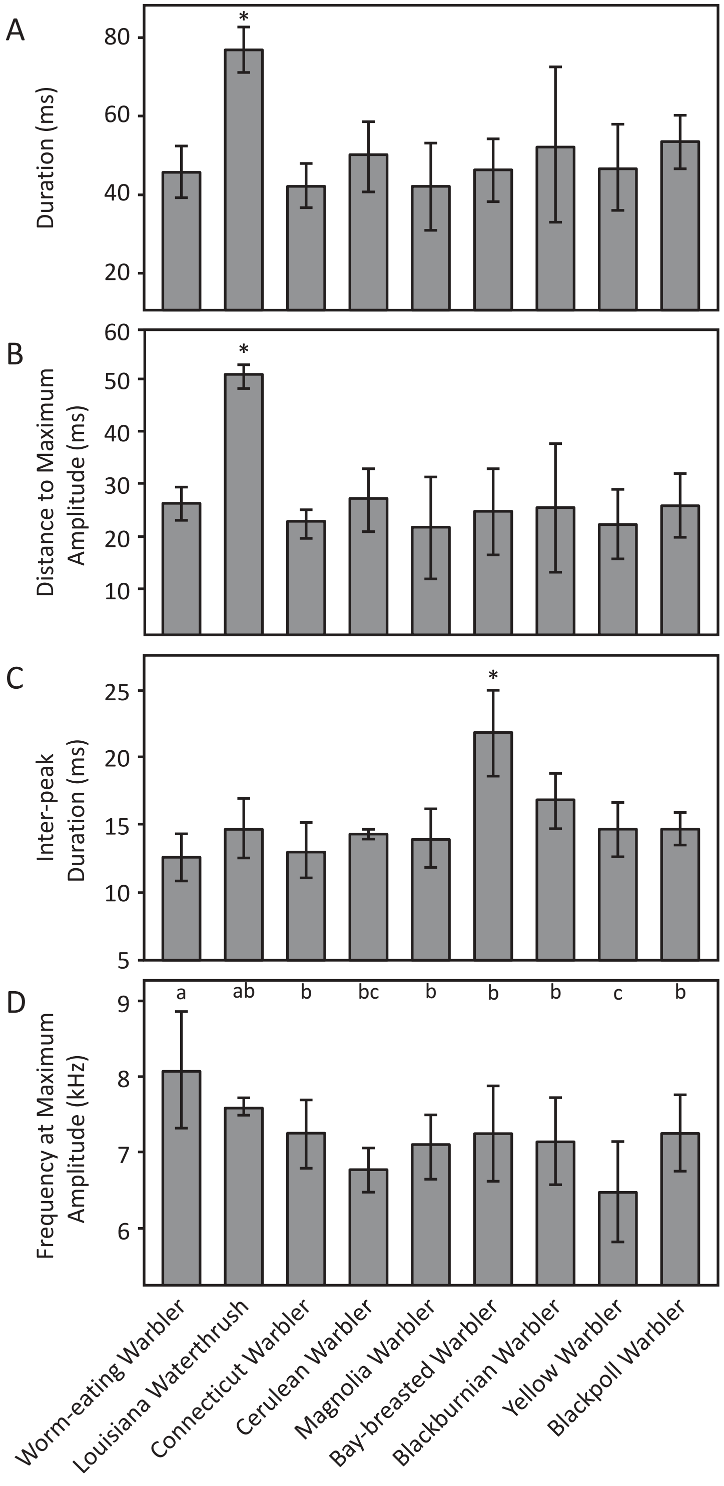

**Figure 3.** Variation in nocturnal flight calls of nine Parulidae warblers in flight call duration (a), distance from start of call to point of maximum amplitude (b), inter-peak duration (c), and frequency of maximum amplitude (d). Asterisks in (a) through (c) show species that were significantly different from all others based on Tukey's *Post Hoc* tests. Letters in (d) show results of Tukey's *Post Hoc* test, where species not connected by the same letter are significantly different.

the eight other species (Figure 3(b); Tukey's *post hoc* test: q = 3.14; $p \leq 0.001$). The eight remaining species showed no significant difference in distance to maximum amplitude. The inter-peak duration of flight calls exhibited significant variation between species (ANOVA: $F_8 = 34.11$; $p \leq 0.001$): inter-peak duration of Bay-breasted Warbler flight calls was significantly longer than the other species (Figure 3(c); Tukey's *post hoc* test: q = 3.14; $p \leq 0.001$). Also, the peak frequency at maximum amplitude showed significant variation (ANOVA: $F_8 = 10.96$; $p \leq 0.001$): Worm-eating Warbler calls were significantly higher in peak frequency at maximum amplitude than all other species except Louisiana Waterthrush (Figure 3(d); $p < 0.05$).

The nine species exhibited notable differences for multiple frequency measurements: minimum frequency (ANOVA: $F_8 = 8.07$; $p \leq 0.001$), peak frequency at maximum amplitude (ANOVA: $F_8 = 10.96$; $p \leq 0.001$), and peak frequency at end (ANOVA: $F_8 = 9.69$; $p \leq 0.001$). Both Cerulean Warbler and Yellow Warbler calls were significantly lower in frequency, for several measurements, compared to other species (e.g. Tukey's *post hoc* tests for peak frequency at maximum amplitude: Yellow Warbler vs. Magnolia Warbler q = 3.14, $p \leq 0.001$; Cerulean Warbler vs. Worm-eating Warbler q = 3.14, $p = 0.001$). There was no difference, however, in peak frequency at maximum amplitude between Yellow Warbler and Cerulean Warbler calls (Tukey's *post hoc* test: q = 3.14, $p = 0.98$) or between Cerulean Warbler and Magnolia Warbler calls (Tukey's *post hoc* test: q = 3.14, $p = 0.96$). Cerulean Warbler and Yellow Warbler calls were generally lower in frequency measurements than most species but were not significantly different from one another (Tukey's *post hoc* tests: q = 3.14, $p > 0.40$).

The nine species showed significant interspecific variation in the number of frequency modulations of calls (ANOVA: $F_8 = 10.06$; $p \leq 0.001$). Louisiana Waterthrush and Cerulean Warbler calls contained more modulations than most species. For example, Louisiana Waterthrush calls contained significantly more modulations than seven species: Bay-breasted Warbler, Magnolia Warbler, Blackburnian Warbler, Connecticut Warbler, Worm-eating Warbler, Yellow Warbler and Blackpoll Warbler (Tukey's *post hoc* tests: q = 3.14, $p \leq 0.002$). However, Louisiana Waterthrush and Cerulean Warbler flight calls did not contain different numbers of modulations (Tukey's *post hoc* test: q = 3.14, $p = 0.77$). Further, the rates of frequency modulation (e.g. slope of frequency modulation from minimum to maximum frequency and slope of frequency modulation from start to first frequency peak) did reveal significant variation between species (ANOVA: $p \leq 0.001$) although there were no notable differences between species in the post-hoc analyses (Tukey's *post hoc* tests: q = 3.14, $p > 0.07$).

Five species (Worm-eating Warbler, Louisiana Waterthrush, Cerulean Warbler, Bay-breasted Warbler and Yellow Warbler) were significantly different from the remaining four and could be distinguished based on one or more acoustic properties in this dataset (Figure 4). Only calls produced by two species (Worm-eating Warbler and Louisiana Waterthrush) could be unambiguously assigned to species in all cases.

## *Canonical discriminant analysis*

A forward stepwise canonical discriminant analysis of the flight calls of six species of warbler classified 73% of 159 calls to the correct species based on 14 fine structural

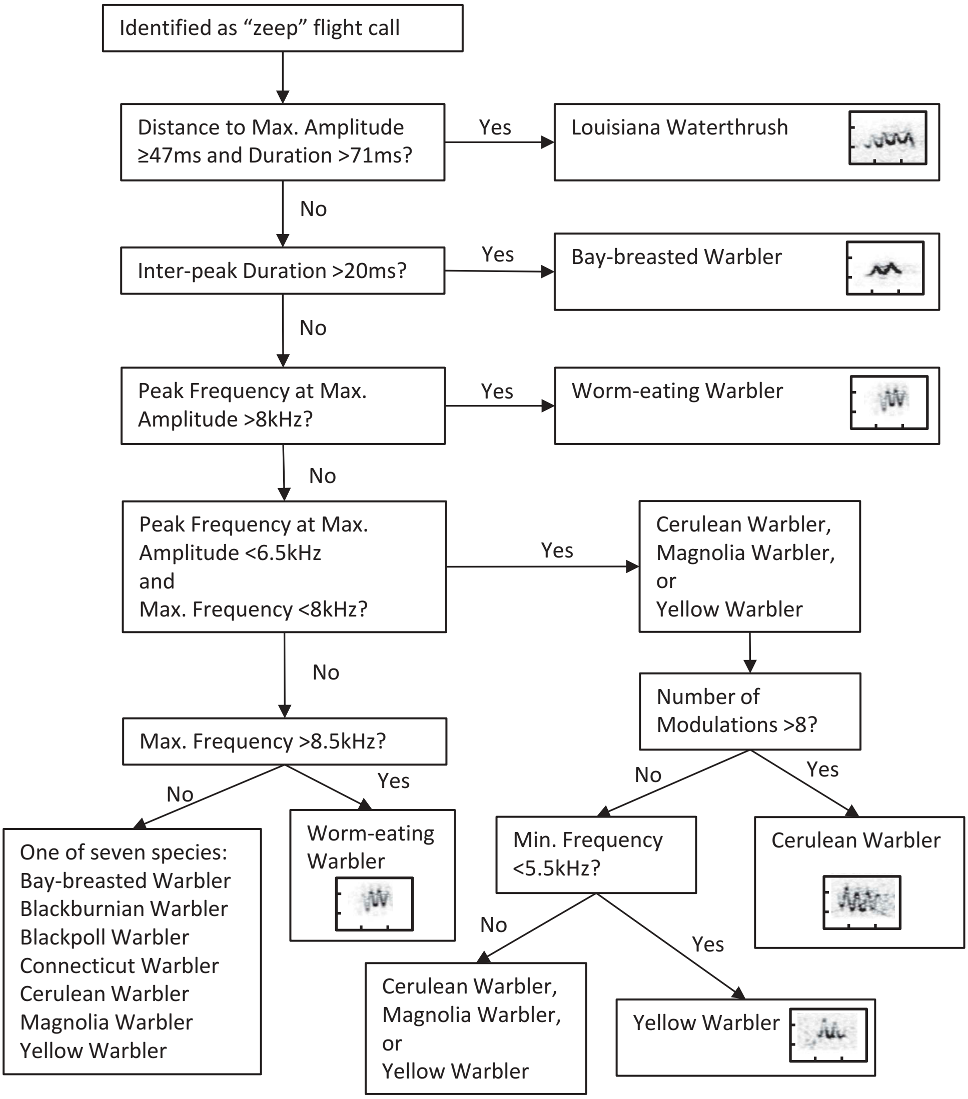

**Figure 4.** Flow chart for assigning species identity to nocturnal flight calls of birds in the 'zeep' flight call complex, based on recordings of 178 animals held for banding at banding stations in Ontario, and select calls from existing sound libraries. The calls of five species could be identified to the species level using one or more acoustic properties in this dataset. Only two species (Worm-eating Warbler and Louisiana Waterthrush) could be unambiguously assigned to species in all cases. Some species have more than one end-point (e.g. Worming-eating Warbler), if their calls have features that span a broad range, and sometimes they can be distinguished to the species level (e.g. a Bay-breasted Warbler with an inter-peak duration of > 20 ms is diagnostic) and other times they cannot (e.g. Bay-breasted Warbler with an inter-peak duration of < 20 ms could be a Bay-breasted Warbler, Blackburnian Warbler, or Blackpoll Warbler).

properties (cross-validation: 68.6% assigned correctly; Figure 5). The five acoustic features selected by the model were inter-peak duration, maximum frequency, slope of frequency modulation from start to first peak, peak frequency at maximum amplitude and number of modulations, respectively. In spite of the 27% misclassification rate,

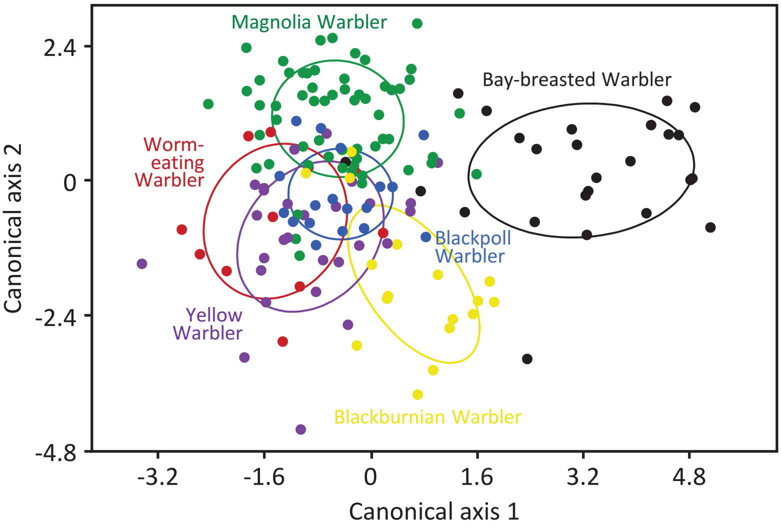

**Figure 5.** Plot of first two canonical axes produced by canonical discriminant analysis using 14 acoustic measurements. Dots represent nocturnal flight calls from six warbler species. Circles represent 50% confidence ellipses. High values for canonical axis 1 were associated with long inter-peak duration and increased slope of frequency modulation from start to first frequency peak. High values for canonical axis 2 were associated with short distance to maximum amplitude and high maximum frequency.

the 73% accuracy of the canonical discriminant analysis was significantly higher than the 36.1% level of correct assignment by chance (Binomial test: $p \leq 0.001$). Spectral-temporal measurements with strongest loadings on the first two canonical axes included the inter-peak duration, maximum frequency, and the peak frequency at maximum amplitude of the call.

Canonical discriminant analysis correctly identified 85% (51 out of 60) and 84% (21 out of 25) of Magnolia Warbler and Bay-breasted Warbler flight calls, respectively. Magnolia Warblers, however, were represented considerably more often in the

**Table 3.** Mean similarity values produced from pairwise spectrographic cross-correlation of the nocturnal flight calls of nine warbler species (i.e. ‘zeep’ complex”). Spectrographic cross-correlation scores showed flight calls of seven species to be more similar to conspecific calls than the calls produced by heterospecific birds.

| Species | Number of calls (Within) | Similarity within species (mean± SD) | Similarity between species (mean± SD) | Within-versus-between species comparison |
|---|---|---|---|---|
| Worm-eating Warbler | 11 | 0.60 ± 0.025 | 0.29 ± 0.095 | $W_{10} = -33$, $p = 0.001$ |
| Louisiana Waterthrush | 8 | 0.27 ± 0.105 | 0.29 ± 0.107 | $t_7 = 0.98$, $p = 0.36$ |
| Connecticut Warbler | 7 | 0.60 ± 0.054 | 0.40 ± 0.042 | $t_6 = 12.5$, $p < 0.0001$ |
| Cerulean Warbler | 4 | 0.68 ± 0.035 | 0.39 ± 0.016 | $t_3 = -18.0$, $p = 0.0004$ |
| Magnolia Warbler | 60 | 0.50 ± 0.088 | 0.37 ± 0.050 | $W_{59} = -848.0$, $p < 0.0001$ |
| Bay-breasted Warbler | 25 | 0.39 ± 0.063 | 0.38 ± 0.050 | $W_{24} = -91.5$, $p = 0.0106$ |
| Blackburnian Warbler | 17 | 0.43 ± 0.071 | 0.38 ± 0.035 | $W_{16} = -59.5$, $p = 0.0032$ |
| Yellow Warbler | 28 | 0.32 ± 0.055 | 0.32 ± 0.121 | $W_{27} = -11.0$, $p = 0.81$ |
| Blackpoll Warbler | 18 | 0.58 ± 0.137 | 0.37 ± 0.035 | $W_{17} = -82.5$, $p < 0.0001$ |

[a] W-values represent Wilcoxon matched-pairs signed-rank test and t-values represent paired t-test

analysis (60 out of 159 calls). The analysis showed mixed levels of accuracy when classifying the four remaining species. Canonical discriminant analysis revealed the lowest accuracy when classifying Blackpoll Warbler flight calls (33% identified correctly), which were misidentified as Magnolia Warbler calls 44% of the time. Connecticut Warbler, Cerulean Warbler and Louisiana Waterthrush were not included in the discriminant analysis due to small sample sizes.

### Spectrographic cross-correlation

Spectrographic cross-correlation scores for seven warblers were significantly higher for within-species versus between-species comparisons (Table 3). Of the two remaining species, Yellow Warbler calls showed similar spectrographic cross-correlation scores for within-species versus between-species (Table 3). Spectrographic cross-correlations showed the calls of Louisiana Waterthrush to be slightly more similar to heterospecific calls rather than calls produced by their own species, however this difference was not significant (Table 3).

## Discussion

Recordings of nocturnal flight calls of migratory birds hold the potential to be a useful tool for nocturnal migration monitoring, depending on the reliability of accurate assignment of calls to species. In our analysis of the species-specific features of nocturnal flight calls of nine species in the ‘zeep’ call complex, we found that three bioacoustic comparison techniques revealed significant variation in acoustic structure between species. Analysis of variance of fine structural details of flight calls showed significant variation between species for all 14 variables, although post-hoc analysis showed significant species-to-species differences for only several variables and species. Canonical discriminant analysis of fine structural properties assigned calls to the correct species at levels significantly higher than statistical chance, although not with perfect accuracy. Further, spectrographic cross-correlation revealed within-species similarity scores that were significantly higher than between-species scores for seven out of nine species. Taken together, these results provide support for the hypothesis that the nocturnal flight calls of warblers in the ‘zeep’ complex exhibit specifies-specific differences in fine structural features. Whereas several species may be classified with confidence on the basis of their nocturnal flight calls, our results suggest that many species can be classified only with moderate confidence, with some classification error. Therefore, the use of nocturnal flight calls to differentiate species within the ‘zeep’ complex must be done cautiously and with recognition of the potential for classification errors.

Our analysis of variance of 14 acoustic measurements revealed notable differences in fine structure of these calls between species. Five species, Worm-eating Warbler, Louisiana Waterthrush, Cerulean Warbler, Bay-breasted Warbler and Yellow Warbler, were significantly different from others and able to be distinguished based on one or more acoustic properties (Figure 4). Worm-eating Warbler and Louisiana Waterthrush flight calls were the only ‘zeep’ calls able to be differentiated in all cases. In particular, Louisiana Waterthrush flight calls are significantly longer in duration and distance to maximum amplitude, and Bay-breasted Warbler flight calls have significantly longer inter-peak duration. As a result, ‘zeep’ calls with a duration of > 75 ms and distance to maximum amplitude of ≥ 47 ms may be reliably identified as Louisiana Waterthrush, and calls with an inter-peak duration of > 20 ms can be reliably identified as Bay-breasted Warbler. Further, species exhibited other notable differences in structural details between species. For example, Cerulean Warbler and Yellow Warbler flight calls were typically lower in frequency than other species but were not significantly different from one another and therefore cannot reliably be distinguished on the basis of frequency characteristics alone.

Our results indicate there are acoustic differences between these calls that allow the differentiation of some members of the ‘zeep’ complex based on structural details. Past nocturnal flight calls studies have grouped these species together due to the similarities in fine structure and the limited information we have for these calls (e.g. Sanders and Mennill 2014b). This practice of classifying nocturnal flight calls into catch-all bioacoustic categories has inhibited the collection of species-specific population data on many bird species including the nine ‘zeep’ warblers. Separation of the ‘zeep’ flight calls would allow biologists to use passive acoustic monitoring to collect detailed information on the populations of these nine warblers, including multiple species of conservation concern (e.g. Louisiana Waterthrush, Cerulean Warbler and Worm-eating Warbler). It is worthwhile to recognize that atmospheric properties (e.g. temperature and humidity) can affect the transmission of flight calls, influencing the measured values of the call properties of interest (Horton et al. 2015b). Consequently, caution when identifying nocturnal flight calls is necessary since atmospheric properties have the potential to confound the identification of birds in flight. Future research exploring the effect of temperature and humidity on transmission of nocturnal flight calls would be valuable.

Despite the differences in fine structure, there has been no research to date that has investigated whether these warblers are able to differentiate the flight calls within the ‘zeep’ species-group. Many bird species are able to communicate information about the caller in other types of calls, including species-identity in the alarm calls of many passerine birds (e.g. European Robin, *Erithacus rubecula*, Davies et al. 2004; Reed Warbler, *Acrocephalus scirpaceus*, 2004). Moreover, diverse bird species have demonstrated a high capacity for discerning differences in the fine structure of calls (e.g. individual recognition of King Penguin parents’ calls, *Aptenodytes patagonicus*; Jouventin et al. 1999; kin recognition in contact calls of Long-tailed Tits, *Aegithalos caudatus*; Sharp et al. 2005). The ability of migratory birds to discern their nocturnal flight calls could potentially provide fitness benefits. The nine ‘zeep’ warblers exhibit differences in habitat preferences and migration timing (Francis and Cooke 1986; Schieck and Song 2006) and differences in call structure could serve a role in facilitating conspecific recognition during migration. Many warbler species participate in mixed species flocks during migration and may not have the necessity (or ability) to discern these calls (Rodewald and Brittingham 2002). The differences in fine structure between species may be the result of different ecological pressures acting on the fine structure of flight calls for maximum propagation of sound within habitats that the birds are most strongly associated with (Morton 1975; Farnsworth and Lovette 2008).

The canonical loadings of our discriminant analysis suggest that inter-peak duration, peak frequency at maximum amplitude and maximum frequency are important structural features for distinguishing these calls. There remains, however, a substantial level of misclassification (27%) in our discriminant analysis for some species (e.g. Blackpoll

Warbler) and multiple misclassifications for all six included species. Several factors may have contributed to this level of misclassification. Notably, our analyses suffered from small and unequal sample sizes for uncommon and cryptic species that are not captured regularly by mist-netting efforts in our study area. Many of the birds that were captured and placed in our recording apparatus (> 70%) did not produce flight calls during the 5-min recording period and therefore could not be included in our analysis. The limited sample sizes of three rarer species (Connecticut Warbler, Cerulean Warbler and Louisiana Waterthrush) made it impossible to include all nine species in all three comparison analyses in order to avoid violating the assumptions of canonical discriminant analyses (Cohen et al. 2013). The limited sample sizes for certain species highlights the need for the collection of a more comprehensive library of nocturnal flight calls to allow further resolution of flight calls.

Our third spectral comparison approach, spectrographic cross-correlation, revealed differences between seven of nine 'zeep' species. The difference, however, between mean within-species and between-species scores for Bay-breasted Warbler was small though significant. In contrast to our results from the comparison of fine structural properties, Louisiana Waterthrush calls did not differ significantly from heterospecific calls compared to calls produced by conspecific individuals. While Louisiana Waterthrush calls had the lowest reported within-species similarity cross-correlation scores, measurements of structural parameters did not indicate Louisiana Waterthrush calls were more variable than calls produced by other species. Since Louisiana Waterthrush calls were collected from different public sources, recordings possessed varying amounts and types of background noise and may have been recorded with different types of equipment which may have contributed to the low similarity scores. Yellow warbler calls also did not show a difference between conspecific and heterospecific calls. The majority of 'zeep' species had within-species scores that were considerably higher than between-species scores suggesting that spectrographic cross-correlation can be useful in discerning calls from the 'zeep' complex. While our recordings of birds held for banding had very high signal to noise ratio, nocturnal flight call recordings of wild-flying birds generally have poor signal to noise ratio. A lower signal to noise ratio may introduce irrelevant background information into the spectrogram cross-correlation and decrease the accuracy of any similarity analysis, including spectrographic cross-correlation and measurement of fine structural parameters (Ehnes and Foote 2015). As a result, spectrographic cross-correlation is appropriate for comparison of nocturnal flight calls; however, the lower signal to noise ratio typical of flight call recordings and the high degree of intraspecific variation in flight calls (Farnsworth 2005; Farnsworth and Lovette 2008) may lead to potential misclassification by spectrographic cross-correlation. Instead, we recommend the combined use of fine structural properties and spectrographic cross-correlation as an appropriate method for the comparison of nocturnal flight calls. The development of an approach that uses both fine structure and spectrographic cross-correlation, along with the incorporation of migratory timing information (Francis and Cooke 1986; Schieck and Song 2006), would provide a reliable method for identifying species within the 'zeep' species-complex by call. Further, given the current interest in using automated classification to analysing flight calls, the development of an approach for automatic classification using both fine structure and spectrographic cross-correlation could prove promising. A previous attempt of automated identification of flight calls using spectrographic cross-correlation revealed that this approach has potential (Keen et al. 2014).

It is important to develop appropriate procedures for the identification and comparison of other bioacoustic categories of nocturnal flight calls. For example, the ‘up’ species-group consists of seven warblers and two sparrows (Ovenbird, *Seiurus aurocapilla*; Tennessee Warbler, *Oreothlypis peregrina*; Orange-crowned Warbler, *Oreothlypis celata*; Nashville Warbler, *Oreothlypis ruficapilla*; Mourning Warbler, *Geothlypis philadelphia*; Yellow-rumped Warbler, *Setophaga coronata*; Black-throated Green Warbler, *Setophaga virens*; White-crowned Sparrow, *Zonotrichia leucophrys*; and Vesper Sparrow, *Pooecetes gramineus*) that produce flight calls described as a single modulated upsweep that currently cannot be identified to species level (Sanders and Mennill 2014b). In previous studies, biologists have attempted to identify unknown flight calls by narrowing down possibilities based on seasonality and local reports of sightings (Lanzone et al. 2009); however, this increases the risk of misidentification and error within a data set. Since the identification of nocturnally migrating birds represents a primary benefit of acoustic recording over other nocturnal monitoring approaches, it is critical to quantify the variation within and between the nocturnal flight calls of our migratory birds to allow discernment of these calls. Currently, nocturnal flight call monitoring studies cannot meaningfully inform population trends of many species within these bioacoustic categories. Since species that produce structurally similar calls all possess unique natural histories with distinct habitat preferences and migratory strategies, it is critical to determine which flight call characteristics, if any, can be used to discern species identity of other flight call bioacoustic categories in order to allow the collection of species-specific information on these birds.

Our sound comparison techniques revealed species-specificity in the nocturnal flight calls produced by the nine warblers within the ‘zeep’ complex. Our results suggest that duration, inter-peak duration, peak frequency at maximum amplitude and maximum frequency of nocturnal flight calls are useful acoustic properties for distinguishing certain species within the ‘zeep’ complex. This is the first study, to our knowledge, to investigate if acoustic divergence in flight call properties of the ‘zeep’ species-group may allow reliable discernment of these calls. We suggest that spectro-temporal differences in flight calls produced by these species allow the reliable identification of at least five ‘zeep’ species based on acoustic properties. There remains, however, a moderate level of misclassification when identifying the flight calls of seven species, which highlights the need for a comprehensive library of nocturnal flight calls and further resolution of these calls. We suggest the combined use of the three described comparison techniques, combined with information concerning migratory timing, will be a valuable approach for identifying species within the ‘zeep’ complex on the basis of call alone. This study serves to improve the capabilities of nocturnal flight call monitoring through allowing the collection of species-specific information on the populations of at least five migratory songbirds, including two species-at-risk (i.e. Louisiana Waterthrush and Cerulean Warbler).

## Acknowledgements

We thank the staff and volunteers at the Long Point Bird Observatory and Holiday Beach Migration Observatory for field assistance and providing banding data. We thank the Explorers Club and Sigma Xi for student research grants to B.L. and the Natural Sciences and Engineering Research Council (NSERC), Algoma University and the University of Windsor for research grants to J.R.F. and D.J.M. We thank two anonymous reviewers that provided valuable input during the revision of this manuscript.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This work was supported by the Explorers Club; Natural Sciences and Engineering Research Council of Canada; Sigma Xi.

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## References

Acevedo MA, Villanueva-Rivera LJ. 2006. Using automated digital recording systems as effective tools for the monitoring of birds and amphibians. Wildl Soc Bull. 34:211–214.

André M, Van Der Schaar M, Zaugg S, Houégnigan L, Sánchez AM, Castell JV. 2011. Listening to the deep: live monitoring of ocean noise and cetacean acoustic signals. Mar Pollut Bull. 63:18–26.

Baker MC, Logue DM. 2003. Population differentiation in a complex bird sound: a comparison of three bioacoustical analysis procedures. Ethology. 109:223–242.

Blumstein DT, Mennill DJ, Clemins P, Girod L, Yao K, Patricelli G, Deppe J, Hanser SF. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. J Appl Ecol. 48:758–767.

Celis-Murillo A, Deppe JL, Allen MF. 2009. Using soundscape recordings to estimate bird species abundance, richness, and composition. J Field Ornith. 80:64–78.

Cohen J, Cohen P, West SG, Aiken LS. 2013. Applied multiple regression/correlation analysis for the behavioral sciences. Mahwah (NJ): Routledge.

Cortopassi KA, Bradbury JW. 2000. The comparison of harmonically rich sounds using spectrographic cross-correlation and principal coordinates analysis. Bioacoustics. 11:89–127.

Damoulas T, Henry S, Farnsworth A, Lanzone M, Gomes C. (2010). Bayesian classification of flight calls with a novel dynamic time warping kernel. Machine Learning and Applications, 2010The Ninth International Conference on Machine Learning and Applications (ICMLA); Washington, DC; 424–429.

Davies NB, Madden JR, Butchart SHM. (2004). Learning fine-tunes: a specific response of nestlings to parental alarm calls of their own species. Proc R Soc Lond B Biol Sci, *271*, 2297–2304.

Diehl RH, Larkin RP, Black JE. 2003. Radar observations of bird migration over the Great Lakes. Auk. 120:278–290.

Ehnes M, Foote JF. 2015. Comparison of autonomous and manual recording methods for discrimination of individually distinctive Ovenbird songs. Bioacoustics. 24:111–121.

Evans WR, O'Brien M. 2002. Flight calls of migratory birds: eastern North American landbirds (CD-ROM). Ithaca (NY): Oldbird.

Evans WR, Rosenberg KV. 2000. Acoustic monitoring of night-migrating birds: a progress report. In: Bonney RE Jr., Pashley DN, Cooper R, editors. Strategies for bird conservation: The Partners in Flight Planning Process. Proceedings of the 3rd Partners in Flight Workshop; Cape May, NJ; 1995 Oct 1–5.

Farnsworth A. 2005. Flight calls and their value for future ornithological studies and conservation research. Auk. 122:733–746.

Farnsworth A, Gauthreaux SA Jr, Blaricom DV. 2004. A comparison of nocturnal call counts of migrating birds and reflectivity measurements on Doppler radar. J Avian Biol. 35:365–369.

Farnsworth A, Lovette IJ. 2005. Evolution of nocturnal flight calls in migrating wood-warblers: apparent lack of morphological constraints. Journal of Avian Biology. 36:337–347.

Farnsworth A, Lovette IJ. 2008. Phylogenetic and ecological effects on interspecific variation in structurally simple avian vocalizations. Biol J Linnean Soc. 94:155–173.

Fitzsimmons LP, Barker NK, Mennill DJ. 2011. Further analysis supports the conclusion that screaming Piha (*Lipaugus vociferans*) songs are individually distinctive and bear a lek signature. Auk. 128:790–792.

Francis CM, Cooke F. 1986. Differential timing of spring migration in wood warblers (*Parulinae*). Auk. 103:548–556.

Griffiths ET, Keen SC, Lanzone M, Farnsworth A. 2016. Can nocturnal flight calls of the migrating songbird, American redstart, encode sexual dimorphism and individual identity? PloS One. 11:e0156578.

Hamilton WJ. 1962. Evidence concerning the function of nocturnal call notes of migratory birds. The Condor. 64:390–401.

Horton KG, Shriver WG, Buler JJ. 2015a. A comparison of traffic estimates of nocturnal flying animals using radar, thermal imaging, and acoustic recording. Ecological Appl. 25:390–401.

Horton KG, Stepanian PM, Wainwright CE, Tegeler A. 2015b. Influence of atmospheric properties on detection of wood-warbler nocturnal flight calls. Int J Biometerology. 59:1385–1394.

Jouventin P, Aubin T, Lengagne T. 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. Anim Behav. 57:1175–1183.

Keen S, Ross JC, Griffiths ET, Lanzone M, Farnsworth A. 2014. A comparison of similarity-based approaches in the classification of flight calls of four species of North American wood-warblers (Parulidae). Ecol Inform. 21:25–33.

Lanzone M, Deleon E, Grove L, Farnsworth A. 2009. Revealing undocumented or poorly known flight calls of warblers (*Parulidae*) using a novel method of recording birds in captivity. Auk. 126:511–519.

Larkin RP, Evans WR, Diehl RH. 2002. Nocturnal flight calls of Dickcissels and Doppler radar echoes over south Texas in spring. J Field Ornith. 73:2–8.

Morris SR, Horton KG, Tegeler AK, Lanzone M. 2016. Individual flight-calling behaviour in wood warblers. Anim Behav. 114:241–247.

Morton ES. 1975. Ecological sources of selection on avian sounds. Am Nat. 109:17–34.

Parker TA. 1991. On the use of tape recorders in avifaunal surveys. Auk. 108:443–444.

Payne KB, Thompson M, Kramer L. 2003. Elephant calling patterns as indicators of group size and composition: the basis for an acoustic monitoring system. Afr J Ecol. 41:99–107.

Penone C, Le Viol I, Pellissier V, Julien JF, Bas Y, Kerbiriou C. 2013. Use of large-scale acoustic monitoring to assess anthropogenic pressures on *orthoptera* communities. Conservation Biol. 27:979–987.

Rodewald PG, Brittingham MC. 2002. Habitat use and behavior of mixed species landbird flocks during fall migration. Wilson Bull. 114:87–98.

Russo D, Jones G. 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. Ecography. 26:197–209.

Sanders CE, Mennill DJ. 2014a. Acoustic monitoring of migratory birds over Lake Erie: avian responses to barriers and the importance of islands. Can Field-Naturalist. 128:135–144.

Sanders CE, Mennill DJ. 2014b. Acoustic monitoring of nocturnally migrating birds accurately assesses the timing and magnitude of migration through the Great Lakes. The Condor. 116:371–383.

Schieck J, Song SJ. 2006. Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: literature review and meta-analyses. Can J For Res. 36:1299–1318.

Sharp SP, McGowan A, Wood MJ, Hatchwell BJ. 2005. Learned kin recognition cues in a social bird. Nature. 434:1127.

Swiston KA, Mennill DJ. 2009. Comparison of manual and automated cross-correlation methods for identifying target sounds in continuous audio recordings of Pileated, Pale-billed, and putative Ivory-billed Woodpeckers. J Field Ornith. 80:42–50.

Taylor A. 1995. Bird flight call discrimination using machine learning. J Acoust Soc Am. 97:3370.