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REVEALING UNDOCUMENTED OR POORLY KNOWN FLIGHT CALLS OF WARBLERS (PARULIDAE) USING A NOVEL METHOD OF RECORDING BIRDS IN CAPTIVITY

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Abstract.—Flight calls are commonly produced by nocturnal migrant birds. Uncertain or unknown identities and lack of information about inter- and intraspecific variation in call notes limit the usefulness of flight calls in monitoring bird populations. We developed a novel method for recording flight calls of temporarily captive birds that allows us to study inter- and intraspecific variation in call notes of birds of known identity, age, and sex. We recorded calls and analyzed data from 13,271 flight calls recorded from 469 individuals of 28 warbler species (Parulidae) over a two-year period. Principal coordinate ordination of spectral cross-correlation data on 7 of the 28 species indicated that flight calls recorded in captivity are similar to those recorded from wild birds. Visual and aural comparisons of species' flight calls from these two different types of recordings support these results. Additionally, we verified flight calls previously identified primarily on inferential evidence and report on previously undocumented flight calls. This method quickly provides many high-quality recordings of the flight calls of individuals of known age and sex, and the results of our analyses greatly facilitate the development of automated sound-analysis algorithms critical for implementing and strengthening future acoustic monitoring applications. *Received 22 September 2008, accepted 16 January 2009.*

Key words: acoustic, flight calls, individual, migration, monitoring, Parulidae, recording, variation, warblers.

El Uso de un Método Novedoso para Grabar Vocalizaciones de Aves en Cautiverio Revela Llamadas de Vuelo No Documentadas o Pobremente Conocidas en las Reinitas (Parulidae)

Resumen.—Las aves migratorias nocturnas comúnmente emiten llamadas de vuelo. Las identidades inciertas o desconocidas y la falta de información sobre la variación intra- e interespecífica en las notas de las llamadas de vuelo limita su utilidad para monitorear las poblaciones de aves. Desarrollamos un método novedoso para grabar las llamadas de vuelo de aves temporalmente cautivas que permite estudiar la variación inter- e intraespecífica en las notas de las llamadas de aves de identidad, edad y sexo conocidos. Grabamos llamadas y analizamos datos de 13,271 llamadas de vuelo emitidas por 469 individuos de 28 especies de reinitas (Parulidae) a lo largo de dos años. Análisis de ordenación de coordenadas principales basados en datos de correlación cruzada de espectros para siete de las 28 especies indicó que las llamadas de vuelo grabadas en cautiverio son similares a las grabadas de aves silvestres. Las comparaciones visuales y auditivas de las llamadas de vuelo de las especies a partir de esos dos tipos diferentes de grabaciones apoyan esos resultados. Además, verificamos la identidad de llamadas de vuelo que habían sido identificadas previamente con base primariamente en evidencia inferencial y documentamos algunas llamadas de vuelo que no habían sido reportadas anteriormente. Este método provee, de forma rápida, muchas grabaciones de alta calidad de las llamadas de vuelo emitidas por individuos de edad y sexo conocidos. Además, los resultados de nuestros análisis facilitan sustancialmente el desarrollo de algoritmos automatizados para analizar sonidos que son críticos para implementar y fortalecer aplicaciones de monitoreo acústico en el futuro.

Flight calls are simple vocalizations that birds use primarily during sustained periods of flight (Evans and O'Brien 2002). These calls are the only means for readily identifying species' passage during nocturnal migration, but a lack of knowledge about many basic features of flight calls limits our ability to use them to monitor vocal migrants. Our understanding of the functions, ontogeny, and origins of flight calls is still imperfect (Farnsworth 2005, Farnsworth and Lovette 2008), and the absence of data on individual variation in calls and calling behavior is particularly problematic for use of flight calls in monitoring.

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Understanding how flight calls vary within and among species and individuals is key for developing acoustic monitoring protocols to count passing individuals. Evans and O'Brien (2002) described and presented recordings of the flight calls of ~200 species, providing an invaluable resource for studying nocturnal migration. However, this compilation, like nearly all other available recordings of flight calls, has limitations for monitoring because of limited data (or no data, for many species) on individual variation.

The current library of available flight-call recordings in North America is limited in three ways: recordings represent species that occur primarily east of the Rocky Mountains (Evans and O'Brien 2002); recordings of some species lack diurnal confirmation, with nocturnal recordings representing the only known examples of flight calls (Evans and O'Brien [2002] and Farnsworth [2005] summarized the methods of flight-call identification); and some species are represented by only a small sample size (e.g., Hooded Warbler [*Wilsonia citrina*] and Swainson's Warbler [*Limnothlypis swainsonii*]; Evans and O'Brien 2002). Methods to expand and rapidly update the existing flight-call library with recordings of absent and underrepresented species would greatly enhance and advance the study of flight calls and the nocturnal migration of passerines.

Most current methods for recording flight calls are summarized in Farnsworth (2005). These methods include using shotgun microphones to record birds during diurnal morning flights or migratory and nonmigratory foraging behaviors (Evans and O'Brien 2002, Farnsworth 2007; for descriptions of morning flight, see Hall and Bell 1981, Wiedner et al. 1992), as well as parabolic antennae and pressure-zone microphones (Graber and Cochran 1959, Evans 1994, Evans and Mellinger 1999, Larkin et al. 2002, Farnsworth et al. 2004). These methods yield high-quality recordings, but they are labor-intensive and can require years to gather a small sample size of correctly identified flight calls (but for special cases, see Evans 1994, Evans and Mellinger 1999, Evans and Rosenberg 2000). Furthermore, gathering certain types of ancillary data (especially individual-specific data such as age, sex, energetic condition, and genetic material) for the calling bird is difficult or impossible. Identification errors during field recording are possible, even for experienced observers (M. O'Brien pers. comm.). Passerines held in captivity during migratory periods vocalize only occasionally (S. Emlen pers. comm., S. A. Gauthreaux pers. comm., C. J. Ralph pers. comm.), and recent attempts to obtain recordings of flight calls from captive birds of known species held overnight in cages during migratory periods met with limited success. For example, over the course of 13 days, attempts to record flight calls from 55 birds using this method yielded recordings of only eight flight-call notes (M. Lanzone and A. Farnsworth unpubl. data). However, many birds held in captivity respond to flight calls of conspecifics flying overhead (M. Lanzone unpubl. data).

Here, we report a novel method for collecting previously undocumented or poorly documented flight calls, documenting species with unconfirmed identity, and increasing knowledge of individual variation in flight calls. We also present the first spectrographic representations of flight calls that were previously undocumented or only hypothetically or phonetically described.

METHODS

We tested the effectiveness of broadcasting flight calls to stimulate calling in captive birds at Powdermill Avian Research Center in southwestern Pennsylvania. Playback of recordings of flight-call notes often elicited calls from the birds held for banding. To exploit this behavior, one of us (M.L.) designed a portable recording chamber (RC) to facilitate recording of flight-call notes given in response to playback.

The RC (Fig. 1) is an opaque, soft-sided cylinder with a small, sealable opening at the top and a microphone incorporated into the base. A pressure-zone microphone (Knowles EK3029c element sensitive in the 2–6 kHz frequency range), similar to the design of the microphone used for other nocturnal recording studies (Evans and Mellinger 1999, Larkin et al. 2002, Farnsworth et al. 2004), was positioned in the bottom of the cone. Using a configuration similar to that used by Farnsworth et al. (2004), we connected the microphone to a Sound Devices MixPre (a microphone pre-amp to boost audio signal to line level) and then to a Terapin Mine TX2000 (a multimedia device that stores, records, and plays digital sound data). We recorded wave files at 22,050 Hz sampling rate and 16-bit sample size and named and saved the files individually by species, band number, age, sex, and date. Pre-amp gain levels were set to avoid clipping recorded calls by calibrating against prerecorded flight calls at different volumes.

After banding and measuring birds, we placed one in each of four RCs. We exposed these birds to prerecorded conspecific and congeneric flight calls (Lovette and Bermingham 2002, Farnsworth and Lovette 2005). We used Evans and O'Brien's (2002) and our own recordings of flight calls, played through a computer speaker ~1.3 m from the RC. Flight-call recordings were played in an identical, predetermined sequence for each species. The time of responses by birds in the RC was noted so that these could be

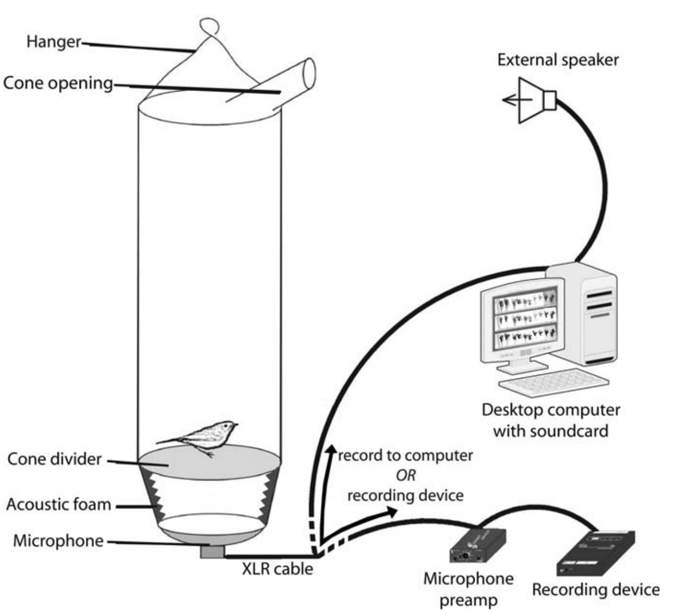

FIG. 1. Portable recording chamber designed for recording vocalizations of passerine birds.

related back to any specific playback stimulus that preceded the response. We recorded sound files for each bird for 2–5 min. Following these recording sessions, we released birds outdoors and recorded any flight calls given upon release using a Sennheiser MKH-70 P40 microphone.

A portable version of the RC setup described above was used to record flight calls of warbler species (Parulidae) of the western United States in August 2005 in the Mogollon Rim and Chiricahua Mountains of Arizona. Because published recordings of flight calls of western U.S. birds are nonexistent, we created playback files of known flight calls from related, eastern species (Lovette and Bermingham 2002) and the few flight calls available for western species (A. Farnsworth unpubl. data). We arranged these calls to create flight-call sequences of longer duration similar to those recorded under typical migration conditions (for examples, see Evans and O'Brien 2002).

We generated spectrograms (Hamming window, 87.5% overlap, 256-point fast Fourier transform, 256-point frame length, and 22,050-kHz sampling rate, resulting in temporal and frequency resolutions of 11.6 ms and 112 Hz, respectively) using RAVEN, version 1.2.1 (Charif et al. 2004), to depict differences in frequency and time characteristics of the recorded flight calls. We also used spectrograms for spectrographic cross-correlation and principal coordinate ordination technique (SPCC-PCO; Clark et al. 1987; Cortopassi and Bradbury 2000, 2006; Farnsworth 2007) to compare flight-call recordings from captive individuals with previously published recordings from migratory periods of free-flying birds of the same species (Evans and O'Brien 2002). The SPCC technique measures the similarity between pairs of calls (Clark et al. 1987, Cortopassi and Bradbury 2000). The process returns a single value between 0 and 1, where 0 represents no similarity and 1 represents identical sounds. The pairwise similarity matrix is then ordinated using principal coordinate analysis to generate a set of latent acoustic measures for each call.

We used latent SPCC-PCO measures to compare calls quantitatively within and among individuals of the same species. The SPCC-PCO analysis was performed in MATLAB, version 7.1, release 14 (Mathworks, Natick, Massachusetts), using a custom program written by K. Cortopassi (SOUNDXT, version 1.2; K. Cortopassi unpubl. data; implemented in Cortopassi and Bradbury 2000, 2006) directly on the call clips generated using RAVEN. We used SOUNDXT to calculate peak correlation coefficients for all pairs of flight calls of seven species—Black-and-white Warbler (*Mniotilta varia*), Tennessee Warbler (*Vermivora peregrina*), Magnolia Warbler (*Dendroica magnolia*), Ovenbird (*Seiurus aurocapilla*), Hooded Warbler, Canada Warbler (*W. canadensis*), and American Redstart (*Setophaga ruticilla*)—across time and frequency. Whereas most previous applications of SPCC involved correlation along time only, it was necessary for our study to allow sliding along the frequency axis as well. The same flight-call pattern within individuals and species may shift up or down in frequency, so to find meaningful spectrogram correlations it was essential that we allow for frequency shifting. We used a maximum time-lag equal to the duration of the longest flight call in milliseconds and a maximum frequency lag of ±3,000 Hz. We chose this lag on the basis of previous visual inspection confirming that calls did not vary in center frequency or bandwidth by more than this amount. We cross-correlated flight calls, which yielded species-specific symmetrical correlation matrices, each containing unique pairwise peak correlation values, to generate a set of species-specific pairwise similarity matrices.

We extracted five principal coordinates from each species' SPCC-generated similarity matrix using the PCO analysis option of the SPCC-PCO tool. Principal coordinate ordination analyses of similarity-distance matrices generate latent orthogonal measures (Gower 1966, 1987; Neff and Marcus 1980; Legendre and Legendre 1998; Everitt and Dunn 2001). Here, they generated latent acoustic measures useful for grouping sounds and associating sounds with extrinsic variables (Cortopassi and Bradbury 2000, Baker 2004). In these analyses, negative eigenvalues represented <1% of the cumulative variation explained by all eigenvalues, and none of the first five PCOs extracted from our samples contained negative eigenvalues. We plotted the first and second PCOs to depict visual similarity of flight calls between captive and free-flying birds.

Results

Here, we present the data for 13,271 flight calls recorded from 469 vocal individuals of 28 species of warbler (Table 1). Spectrographic analyses of the flight calls recorded in the RC show that, in many species, these vocalizations are similar to flight calls given diurnally and nocturnally in free flight; we present an example of this similarity by depicting eight flight-call examples from each of seven species (Fig. 2). The first four calls in each set of eight were recorded in the RCs, and the other four were recorded in the wild from free-flying birds during migration (Evans and O'Brien 2002). Among and within these birds, similar structure, duration, and frequency are visible for all flight calls. Note, however, that subtle differences are also visible for each species.

The first five PCO axes explained 92.8 ± 0.05% (range: 85.3–99.6%) of the variance in the SPCC similarity matrices (Table 2). Scatterplots of the first and second PCOs also demonstrate the similarities between flight calls of captive and free-flying birds. The PCOs of Black-and-white Warbler, Tennessee Warbler, Magnolia Warbler, Ovenbird, Hooded Warbler, and American Redstart flight calls recorded from free-flying birds fall within the largest cluster of flight calls recorded from captive birds. These patterns of broad overlap highlight an overall similarity of latent measurements that capture the variation among these calls within a species. A different pattern is evident for Canada Warbler: captive and wild birds overlap in distinctly different regions of PCO space, and wild-type calls fall in between these overlapping groups. These calls may indicate variation that we did not record from captive birds.

We also spectrographically documented flight calls of five species for the first time: Black-throated Gray Warbler (*D. nigrescens*), Grace's Warbler (*D. graciae*), Red-faced Warbler (*Cardellina rubrifrons*), Lucy's Warbler (*V. luciae*), and Virginia's Warbler (*V. virginiae*) (Fig. 2). Flight calls of Black-throated Gray Warbler are primarily flat in frequency sweep, often exhibiting a slight upsweep at the beginning of the vocalization and a slight downsweep at the end of the vocalization. Some individuals' flight calls exhibit two bands. Flight calls of Grace's Warbler are also primarily flat in frequency sweep, often exhibiting a wide upsweep at the beginning of the vocalization and a rapid modulation of slightly

TABLE 1. Total number of individuals and flight calls of 28 species of warblers (Parulidae) recorded in portable recording chambers by species, sex, and age (AHY = after hatch year, ASY = after second year, HY = hatch year, and SY = second year).

Sex	Female					Male					Unknown						
Age	AHY	ASY	HY	SY	Subtotal	AHY	ASY	HY	SY	Subtotal	AHY	ASY	HY	SY	Subtotal	Grand total	Individuals
Species[a]																	
AMRE	221		159		380	125	40	178		343			4		4	727	20
BBWA			31		31	7		246		253						284	6
BLBW	3				3			105		105						108	2
BLPW			79		79			125		125			17		17	221	9
BTBW			163		163	98		655		753						916	22
BTNW	86		428		514	19		1,103		1,122						1,636	26
BTYW			1		1			9		9						10	4
BWWA	44		13		57	18		75		93						150	9
CMWA			199		199			471		471						670	7
CONW	93				93			8		8						101	3
COYE	33		12		45	89		59		148						193	16
CSWA	13		111	14	138	72		15	9	96			71		71	305	16
GRWA			118		118	19		205		224			30		30	372	31
HOWA			31		31	135		180		315						346	26
KEWA				5	5											5	1
MAWA	281	9	1,138	13	1,441	550	87	499	48	1,184			157		157	2,782	109
MOWA							3			3						3	1
NAWA	284		120		404	396	15	345		756						1,160	31
NOPA			139		139											139	2
NOWA												2	87	34	123	123	7
OVEN						173		3		176	5		455		460	636	18
PAWA			113		113			125		125			24		24	262	7
PAWH													3		3	3	1
PIWA								13		13						13	1
TEWA	81		909		990	1		136		137			302		302	1,429	17
VIWA			13		13	1		50		51			12		12	76	18
YEWA									4	4						4	1
YRWA	44		165		209	42		323		365			23		23	597	58
Total calls	1,183	9	3,942	32	5,166	1,745	145	4,928	61	6,879	5	2	1,185	34	1,226	13,271	469

[a] Warbler species are denoted by four-letter banding codes (Pyle and DeSante 2003). Codes used above as follows: AMRE = American Redstart, BBWA = Bay-breasted Warbler (*Dendroica castanea*), BLBW = Blackburnian Warbler (*Dendroica fusca*), BLPW = Blackpoll Warbler (*D. striata*), BTBW = Black-throated Blue Warbler (*D. caerulescens*), BTNW = Black-throated Green Warbler (*D. virens*), BTYW = Black-throated Gray Warbler, BWWA = Blue-winged Warbler (*Vermivora pinus*), CMWA = Cape May Warbler (*D. tigrina*), CONW = Connecticut Warber (*Oporornis agilis*), COYE = Common Yellowthroat (*Geothlypis trichas*), CSWA = Chestnut-sided Warbler, GRWA = Grace's Warbler, HOWA = Hooded Warbler, KEWA = Kentucky Warbler (*O. formosus*), MAWA = Magnolia Warbler, MOWA = Mourning Warbler (*O. philadelphia*), NAWA = Nashville Warbler, NOPA = Northern Parula (*Parula americana*), NOWA = Northern Waterthrush (*Seiurus noveboracensis*), OVEN = Ovenbird, PAWA = Palm Warbler, PAWH = Painted Redstart (*Myioborus pictus*) , PIWA = Pine Warbler, TEWA = Tennessee Warbler, VIWA = Virginia's Warbler, YWAR = Yellow Warbler (*D. petechia*), and YRWA = Yellow-rumped Warbler (*D. coronata*).

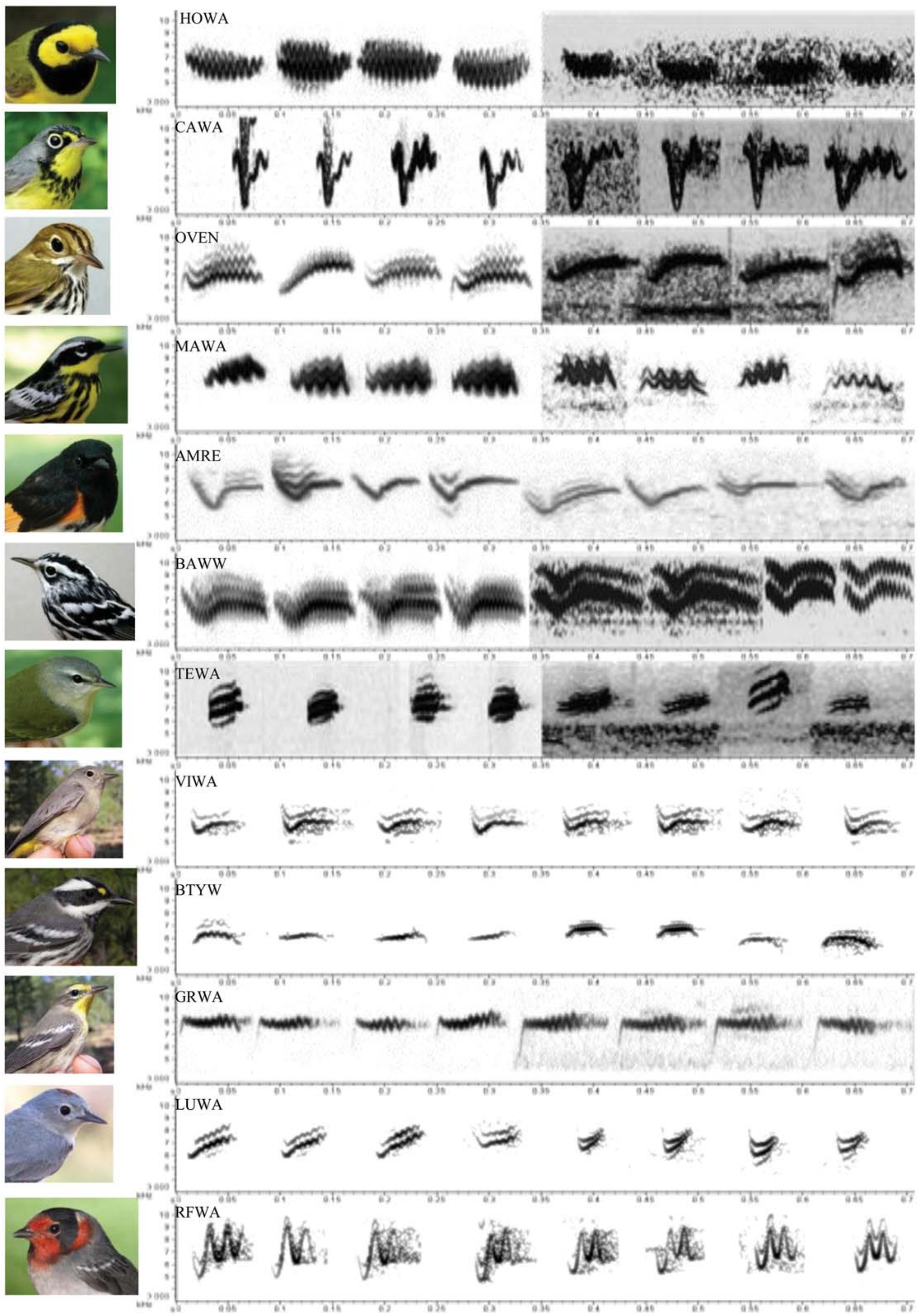

FIG. 2. Example and comparison spectrograms for several warbler species from eastern and western North America. Depicted first are spectrograms for seven eastern species; in each case, the first four examples were recorded in captivity in a portable recording chamber (RC), the other four were recorded from wild, free-flying individuals. Following these are spectrograms for five species of western warblers, recorded from the RC and from free-flying individuals. Species codes are given in Table 1.

Table 2. Top five eigenvalues and associated cumulative goodness-of-fit for principal coordinates extracted from spectrograms of flight calls of seven warbler species (referenced by four-letter code; see footnote of Table 1), including total numbers of calls and individuals for each species.

Species	Eigenvalue	Cumulative goodness-of-fit	Calls (*n*)	Individuals: captive/ wild/total (*n*)
HOWA	1.531	0.526	186	20/4/24
HOWA	0.873	0.697		
HOWA	0.740	0.820		
HOWA	0.479	0.871		
HOWA	0.414	0.910		
AMRE	2.636	0.649	64	12/11/23
AMRE	1.233	0.790		
AMRE	0.948	0.874		
AMRE	0.712	0.922		
AMRE	0.526	0.947		
CAWA	1.989088	0.889365	90	5/12/17
CAWA	0.478457	0.940823		
CAWA	0.304824	0.96171		
CAWA	0.251947	0.975979		
CAWA	0.21613	0.986479		
COYE	5.419	0.915	50	7/19/26
COYE	1.481	0.983		
COYE	0.456	0.990		
COYE	0.340	0.993		
COYE	0.273	0.996		
OVEN	14.076	0.757	323	7/50/57
OVEN	5.758	0.883		
OVEN	3.647	0.934		
OVEN	2.084	0.950		
OVEN	1.741	0.962		
MAWA	10.289	0.620	600	37/45/82
MAWA	5.350	0.788		
MAWA	2.956	0.839		
MAWA	2.424	0.874		
MAWA	2.047	0.898		
TEWA	5.079	0.519	269	29/37/66
TEWA	3.036	0.704		
TEWA	2.097	0.792		
TEWA	1.328	0.828		
TEWA	1.108	0.853		
Mean goodness-of-fit		0.936		
SD		0.052		

increasing depth (in frequency) over the note's duration. All individuals that we sampled exhibited a single band without harmonics or a second note. Flight calls of Lucy's Warbler are slightly rising in frequency sweep, often exhibiting a distinct downsweep at the beginning of the note and some slight modulation at the end of the note. All individuals that we sampled exhibited a second band. Flight calls of Red-faced Warbler show wide, slow, deep modulations, with two peaks in high frequency (a characteristic M shape). However, the note also rises over the course of this modulation. Some individuals that we sampled exhibited a second band. Flight calls of Virginia's Warbler rise in frequency, often exhibiting a slight downsweep at the beginning of the vocalization and modulation over the course of the note. However, some variants show little modulation and markedly shorter durations, and have a more pronounced U-shaped appearance in the spectrograms. All individuals that we sampled exhibited a second band. Time and frequency measurements of the species' flight calls described above can be found in Table 3.

Discussion

Fight calls recorded in the RCs are similar to flight calls recorded diurnally and nocturnally from birds in free flight (Fig. 3). Scatterplots of PCOs indicate that free-flying and captive birds produced flight calls that exhibited similar latent variables for the first two extracted coordinates. The overlap in free-flying and captive birds' flight calls in these plots and the presence of both call types occurring within a 99% confidence interval support this conclusion. However, these plots also showed additional variation within the free-flying and captive birds' flight calls. This is particularly true for Canada Warbler, for which some PCO values from flight calls recorded in the wild did not overlap with any calls recorded in captivity. Although the source of this variation is unknown, we suspect that it may be associated with features of our analysis (e.g., small sample sizes) or warblers' vocal biology (e.g., the potential for subtle variation in call types produced in different scenarios).

The degree to which this method reflects the total individual and species-specific variation in flight calls is unknown. For example, in Chestnut-sided Warblers (*D. pensylvanica*) that responded in the RC ($n = 75$), we did not record a known call type recorded by Evans and O'Brien (2002), but we commonly recorded other known call types. We also recorded individuals of some species producing other types of calls (not known flight calls) that may be examples of previously unknown or unidentified vocalizations. Cataloguing and cross-referencing these call types could lead to future identification of currently unclassifiable calls.

Poorly documented and previously undocumented flight calls represent critical information for improving acoustic monitoring protocols. We verified flight calls previously assigned to species primarily on the basis of inferential evidence (e.g., Hooded Warbler; see Fig. 2). Moreover, we present the first published

Table 3. Mean (± SD) time and frequency measurements for five species of warblers from the western United States (i.e., west of the Rocky Mountains). Four-letter species codes are given in footnote of Table 1.

Species	Duration (ms)	Low frequency (kHz)	Center frequency (kHz)	High frequency (kHz)	Delta frequency (kHz)
BTYW	0.04 ± 0.00	5,999.74 ± 451.34	6,734.02 ± 358.90	7,015.68 ± 321.11	1,015.945 ± 286.16
GRWA	0.06 ± 0.01	6,070.37 ± 741.59	7,622.78 ± 178.62	8,123.65 ± 302.25	2,053.30 ± 690.93
LUWA	0.04 ± 0.01	5,790.83 ± 181.08	6,524.56 ± 228.53	7,430.64 ± 557.46	1,639.79 ± 507.26
RFWA	0.04 ± 0.00	5,207.39 ± 323.54	6,966.01 ± 202.99	9,439.66 ± 271.07	4,232.28 ± 497.66
VIWA	0.04 ± 0.01	6,380.40 ± 370.55	7,407.43 ± 172.26	8,727.51 ± 367.28	2,347.11 ± 606.70

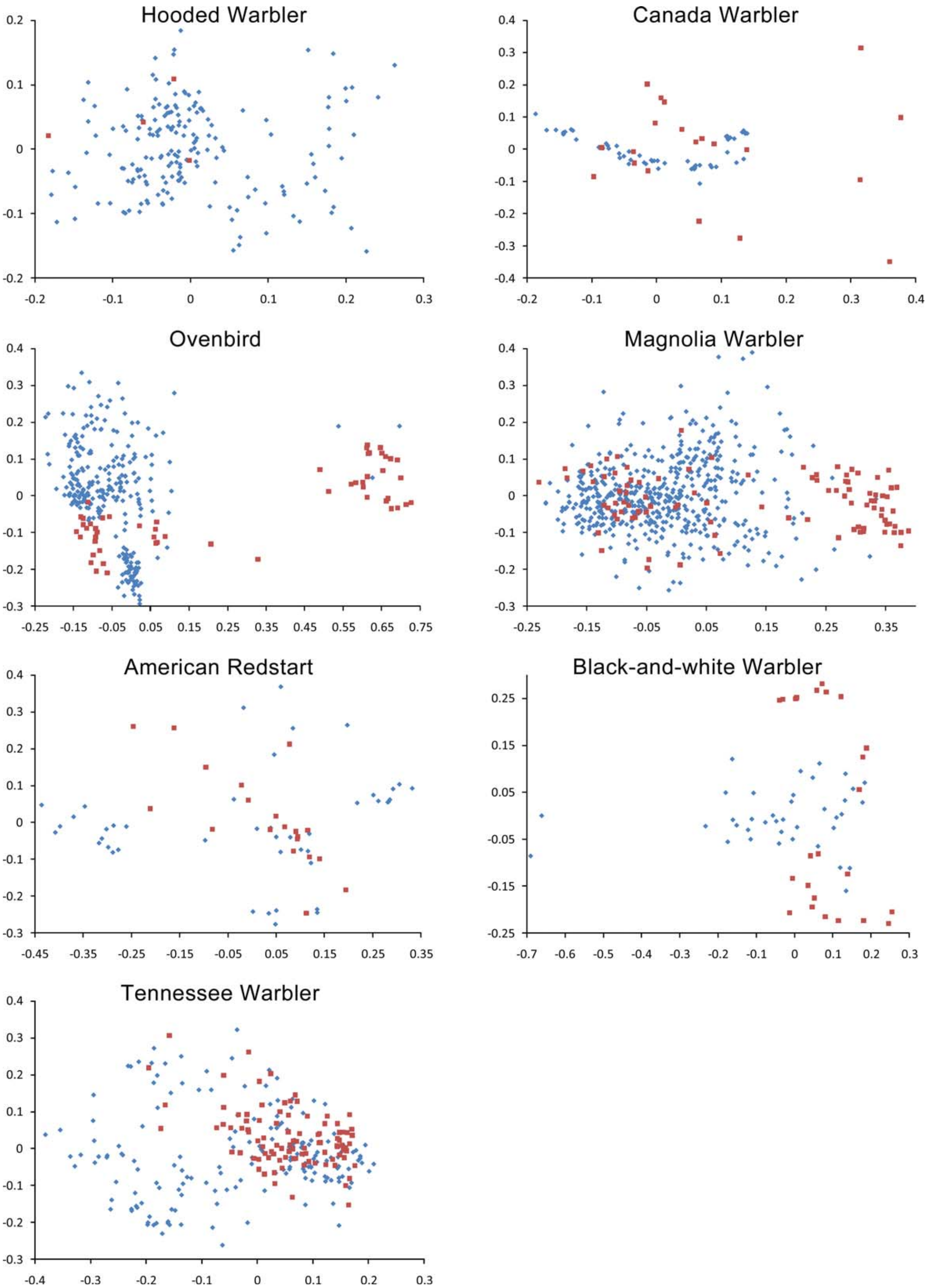

FIG. 3. Principal coordinate ordination scatterplots for seven species of warblers, comparing flight calls of captive and of wild, free-flying individuals (blue diamonds = captive, red squares = wild).

spectrograms for Lucy's, Virginia's, Red-faced, Grace's, and Black-throated Gray warblers. Spectrograms of flight calls from Lucy's and Virginia's warblers are visually similar to those from other species in the genus *Vermivora*, particularly Nashville Warbler (*V. ruficapilla*) and Orange-crowned Warbler (*V. celata*). The characteristic double-banded upsweep (Evans and O'Brien 2002) signature of two rising, nearly parallel notes with rapid frequency modulation is visible. Similarly, spectrograms of flight calls from Grace's and Black-throated Gray warblers are visually similar to those of other species in the genus *Dendroica*, such as Pine Warbler (*D. pinus*), Palm Warbler (*D. palmarum*), and Prairie Warbler (*D. discolor*). These species share simple, flat or slightly convex-shaped notes with fine rapid-frequency modulation. The Red-faced Warbler, although it has a unique flight call, shares some similarities with congeneric species in the genus *Wilsonia* (i.e., Wilson's Warbler [*W. pusilla*] and Canada Warbler). Although all members of this genus have distinct calls, the M-shaped pattern indicating a slower frequency modulation that characterizes Red-faced Warbler is also apparent in the trailing portion of the calls of the other *Wilsonia*.

Although we presented data collected from 469 vocal individuals of 28 species, we recorded 2,113 birds of 45 passerine species over two years. Overall response rate in the RCs was 86% and varied widely, from 15% to 96% among species. Although there were no statistical differences in overall response rate among age classes, between the sexes, or among seasons (data not shown), we have not yet tested for differences in response rate within all species. Nonetheless, our results demonstrate that the RC is an efficient, cost-effective device for quickly recording large, detailed samples of nocturnal flight calls. Few technical issues occurred with the RC operation, but we encountered some problems with the power source for the pre-amps, volume of stimulus playback, and signal sampling-rate errors. To avoid future power-related issues, we suggest using a filtered alternating-current power converter to power the pre-amp. Although the volume of the stimulus did not seem to affect response from the captive birds, we kept the playback volume low to eliminate the problem. However, additional quantitative information on response to playback in relation to volume is necessary.

We recognize that some data associated with free-flying migratory birds (e.g., effects of intra- and interspecific flocking) are not evident from recordings of captive migrants. However, the RC yielded substantially more and higher-quality data, with far less effort, than traditional field methods. Although collecting similar quantities of calls from many species is possible at certain locations in North America during peak migration seasons (see Evans 1994, Evans and Mellinger 1999, Evans and Rosenberg 2000; M. Lanzone et al. pers. obs.), extracting the necessary detailed information about individuals (e.g., age, sex, and body condition) is virtually impossible. The collection of such individual data facilitates detailed analyses in relation to the acoustic properties of flight calls. Data collected in this way will enable robust techniques for monitoring vocal nocturnal migrants, developing automatic detection software, and assessing inter- and intraspecific variation. Additionally, a large flight-call library and associated data set are necessary for implementing and improving future nocturnal applications for monitoring bird populations over a large geographic scale.

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