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Vocal behavior of New World migratory warblers in wintering grounds (Colombia)

Comportamiento vocal de las reinitas migratorias del Nuevo Mundo en zonas de invernada (Colombia)

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Abstract
Migratory birds display distinct ecological behaviors between their breeding and wintering grounds. On breeding grounds, individuals must establish territories, build nests, attract mates, lay eggs, protect the nests, feed the chicks, and raise young. In contrast, wintering grounds are primarily used for foraging and survival, often involving temporary territory use. These ecological differences are thought to result in reduced vocal behavior, and it is widely believed that birds vocalize little or not at all during winter. In this study, I used both Active Acoustic Monitoring (AAM) and Passive Acoustic Monitoring (PAM), coupled with BirdNET automatic detection, to examine the vocal behavior of New World warblers in wintering grounds in Colombia. I assessed which species vocalize, the types and characteristics of vocalizations, their timing, frequency, habitat use, and ecological contexts. I detected five species vocalizing: Blackpoll Warbler, Canada Warbler, Mourning Warbler, Northern Waterthrush, and Tennessee Warbler. These results provide clear evidence that vocal activity persists in tropical wintering areas. These findings highlight the complexity and ecological relevance of winter vocal behavior in migratory birds and underscore the importance of conserving wintering habitats such as those found in Colombia, where vocalizations may support territory defense, social cohesion, or song development.

Keywords
Active Acoustic Monitoring (AAM), automatic detection, migratory birds, Passive Acoustic Monitoring (PAM).

Resumen
Las aves migratorias exhiben comportamientos ecológicos distintos entre sus áreas de reproducción y de invernada. En las zonas de reproducción deben establecer territorios, atraer parejas, proteger sus nidos, y criar a sus polluelos. En cambio, en las áreas de invernada se enfocan principalmente en la alimentación y la supervivencia, a menudo usando territorios temporales. Estas diferencias han llevado a asumir que el comportamiento vocal disminuye o cesa en zonas tropicales. En este estudio utilicé Monitoreo Acústico Activo (MAA) y Monitoreo Acústico Pasivo (MAP), junto con detección automática con BirdNET, para examinar el comportamiento vocal de reinitas migratorias en zonas de invernada en Colombia. Evalué qué especies vocalizan, los tipos y características de sus vocalizaciones, su temporalidad, frecuencia, hábitat y contexto ecológico. Detecté vocalizaciones en cinco especies: *Setophaga striata*, *Cardellina canadensis*, *Geothlypis philadelphia*, *Parkesia noveboracensis* y *Leiothlypis peregrina*. Estos resultados evidencian que la vocalización persiste en zonas tropicales de invernada, desafiando la suposición común de silencio vocal en esta fase. Este estudio resalta la complejidad ecológica de la vocalización en zonas de invernada y la importancia de conservar estos hábitats en Colombia, donde estas vocalizaciones podrían tener funciones clave en la defensa territorial, la organización social o el desarrollo del canto.

Palabras Clave
Aves migratorias, detección automática, Monitoreo Acústico Activo (MAA), Monitoreo Acústico Pasivo (MAP).

Introduction

Boreal migration in the New World refers to the millions of birds in America that yearly fly from breeding grounds to wintering grounds in the Northern Hemisphere winter (Cox, 1985; DeGraaf & Rappole, 1996; Flack *et al*., 2022). Ecological factors and behaviors vary greatly in each ground (Newton, 2023; Rappole, 1995). On breeding grounds, birds have to establish territories, build nests, find and attract mates, lay eggs, protect the nests, feed the chicks, and nurture the fledglings (DeGraaf & Rappole, 1996; Newton, 2023). While in wintering grounds, birds have to focus mainly on foraging and survival by establishing temporary territories (DeGraaf & Rappole, 1996; Newton, 2023). However, bird ecology and the life history of migrant birds in wintering grounds are substantially less studied (Faaborg *et al*., 2010; Jahn *et al*., 2013; Kelsey, 1992) and constitute an important gap in understanding migrant bird systems. Colombia houses around 275 migrant bird species, with 154 being from the Northern Hemisphere (Bayly *et al*., 2016; Gómez *et al*.,

2015). Thanks to their position near the equator and especially their diversity of suitable habitats and food for migratory species (Bayly *et al*., 2016; González *et al*., 2021; Gutiérrez-Carrillo *et al*., 2024), as well as having important corridors for incoming birds (Bayly *et al*., 2023; Cardenas-Ortiz *et al*., 2020).

Vocal communication is essential for bird survival and reproduction (Catchpole & Slater, 2008; Fichtel & Manser, 2010) and facilitates multiple ecological functions, such as territorial interactions, coordination of reproductive activities, paternal care, feeding, predator avoidance, and pair formation and maintenance, among others (Bradbury & Vehrencamp, 1998; Kroodsma & Miller, 2020). As well as individual recognition (Benti *et al*., 2019; Lefevre *et al*., 2001) or kin/group differentiation (Briefer *et al*., 2008; Monteiro *et al*., 2021; Wanker *et al*., 2005). Thus, studying vocal communication can help us understand bird ecology on a broad level, expand on their life history, and help with conservation efforts (Abrahams, 2022; Penar *et al*., 2020). For migrant birds, differences in ecological functions and behavior, as well as environmental variables, such as photoperiod, change the production of vocal signals, especially in wintering birds (Brewer *et al*., 2020; Smith *et al*., 1997). It is widely considered that bird vocal communication is greatly reduced or ceases in wintering grounds, given there is no necessity to establish nesting territories, attract potential mates, or engage in breeding behavior (Rappole, 1995; Walton *et al*., 2011). However, there are records of certain times that some migratory species vocalize in wintering areas, with a variety of possible reasons behind this behavior (Bates, 1992; DeWolfe & Baptista, 1995; Fitzpatrick, 1980; Katti, 2001; Morton & Stutchbury, 2012; Sorensen, 2014; Sorensen *et al*., 2016; Souriau *et al*., 2019). But since studies are limited, there has been a lack of species studied and approaches to assess these theories.

New World Warblers (Passeriformes: Parulidae) are a family comprised of 115 species, with almost half being migratory species that winter in the tropics, where they generally live in tropical moist forests, from lowland rainforest to high-elevation cloud forest (Winkler *et al*., 2020), specially preferring mid-elevations (Gómez *et al*., 2015). Some species have one or two song categories, with some exhibiting complex, extended songs, in addition to calls and flight calls for other functions (Ficken & Ficken, 1962; Spector, 1992). But most (if not all) studies have focused on vocal behavior on the temperate breeding grounds, under the assumption that warblers don't have to vocalize in wintering grounds, or do it really rarely (Keast & Morton, 1980; Rappole, 1995). In this study, I examined the vocal behavior of New World warblers found in wintering grounds in Colombia to assess which species are vocalizing, what types of vocalizations they produce and their characteristics, at what times, how frequently, in which habitats, and in what ecological contexts.

Methods

I performed recordings on two different ProAves natural reserves, which were previously assessed as suitable wintering grounds for migratory warblers, and had several registers on the eBird platform for many of the birds to evaluate. Firstly, Arrierito Antioqueño is a natural reserve located in Antioquia, Colombia, in the municipality of Anorí. It spans from 1250 to 1850 m.a.s.l., comprises Andean moist montane forests, and a temperature of 16-20°C (Fundación Proaves, s. f.-a); recordings in the reserve were conducted between January 10 and 27 of 2025. And secondly, Reinita Cielo Azul is a natural reserve located in Santader, Colombia, in the municipality of San Vicente del Chucurí. It spans from 1500 to 2070 m.a.s.l., comprises Andean moist montane and premontane forests, as well as shaded coffee plantations, and has a temperature of 16-20°C (Fundación Proaves, s. f.-b); recordings in the reserve were conducted between February 2 and 17 of 2025.

Data collection was taken using both active acoustic monitoring (AAM) and passive acoustic monitoring (PAM). For AAM, I used a Zoom H5 Multi-Track Handy Recorder (WAV format; 44.1 kHz; 16 bits) and a Zoom SGH6 shotgun microphone and did daily trails, in different zones and vegetation covers inside both reserves throughout the day, searching with binoculars any migratory warblers doing active vocalizations, and doing directed recordings at them. For PAM, I employed four AudioMoth (v1.1.0, Firmware 1.11.0) automated recording units (ARUs) (Hill *et al*., 2019), configured using AudioMoth Configuration App 1.12.0; all of them were programmed to record at dawn and dusk (05:30-8:30 and 16:00-19:00 UTC-5), recording one hour continuously with five minutes of resting between them, for a total of six daily hours. The sampling rate was 48 kHz, with a medium-high gain, and saved in WAV format. ARUs were placed inside a Ziploc bag and placed at around 3-4m from the ground. All recording units were placed in the same transect 300m apart for three consecutive days and then changed location. I recorded in different vegetation covers and environments, such as deep forests, forest borders, open areas, coffee plantations, and intervened areas.

All recordings were visualized in Raven Pro 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics, 2024) (FFT-length, 512 samples; overlap, 99%; bandwidth, 88.6 Hz; Hann window), and were processed using BirdNET (Kahl *et al*., 2021) a free deep convolutional neural network that automatically detects and identifies bird species using sound spectrographs; it includes 2473 bird species for South America. I chose a confidence score threshold of 0.3 to filter out false positive matches, given that the

environmental conditions (cicadas, running water, wind, etc.) sometimes affect the detectability of the software.

All subsequent analyses were made in R version 4.4.3 (R Core Team, 2025), all automatic detection result tables were imported using Rraven version 1.0.9 (Araya-Salas, 2024), data manipulation and filtering were made using the packages dplyr version 1.1.4 (Wickham et al, 2023), tidyverse 2.0.0 (Wickham *et al*., 2019), stringr 1.5.1 (Wickham, 2023), and lubridate 1.9.4 (Spinu *et al*., 2024). Firstly, I filtered migratory warbler species, then searched each instance of detection in Raven Pro. For each vocalization, I compared them to recordings both in temperate and tropic areas, as well as checked distribution and eBird registers for each species found, to filter any false positives given by the automatic detector. For each relevant vocalization found, I measured the low frequency, high frequency, peak frequency, duration, entropy, the type of vocalization, the number of songs/calls per minute, number of notes per song, the number of calls/songs per session, the date, hour of start, reserve, and vegetation coverage. All data representation was made using ggplot2 3.5.1 (Wickham *et al*., 2025), patchwork 1.3.0 (Pedersen, 2024), and RColorBrewer 1.1-3 (Neuwirth, 2022).

Results

With AAM I obtained seven recordings of visually confirmed birds actively vocalizing, all of them in the Reinita Cielo Azul Reserve. These included three Canada Warblers and four Mourning Warblers. The recordings lasted a minimum of 30 seconds and did not exceed 2 minutes. With PAM I gathered a total of 320 hours of recording over the 6 weeks: 149 hours in the Arrierito Antioqueño reserve and 171 hours in the Reinita Cielo Azul reserve. Initially, BirdNET found 36803 matches from a total of 742 different species, after filtering for migratory warblers, I had 189 matches for 11 different species (Blackburnian Warbler, Blackpoll Warbler, Blue-winged Warbler, Canada Warbler, Kentucky Warbler, Louisiana Waterthrush, Mourning Warbler, Northern Waterthrush, Tennessee Warbler, Wilson's Warbler, and Worm-eating Warbler). After comparing previously recorded species as well as distribution maps, I filtered species that successfully match vocalization structure and distribution in the locations found. I ended up with 5 confirmed species: Blackpoll Warbler, Canada Warbler, Mourning Warbler, Northern Waterthrush, and Tennessee Warbler, which are detailed further (Figure 1).

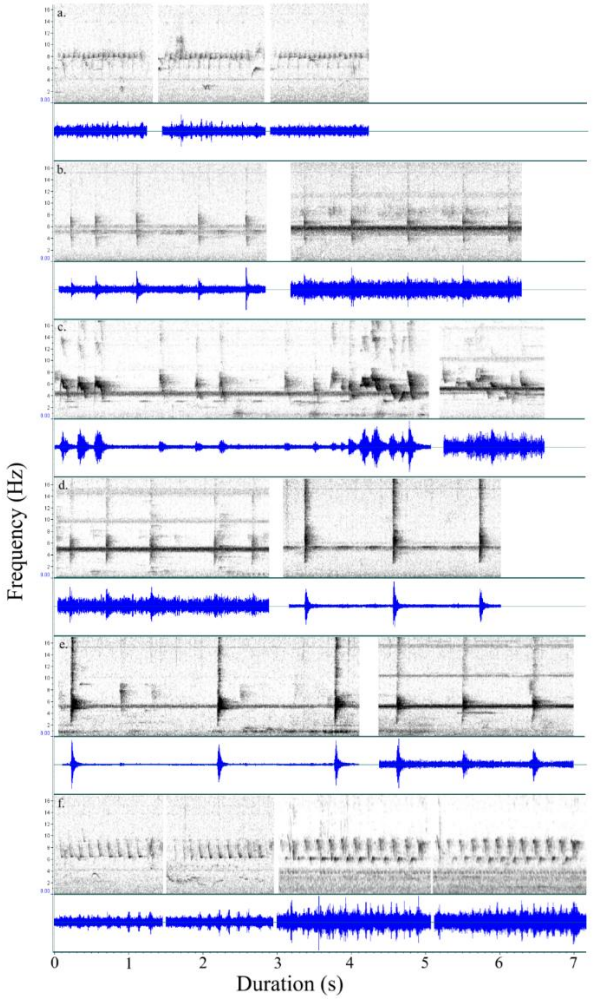

Figure 1. Spectrograms and waveforms showing representative samples of the different vocalizations found: **a.** Blackpoll Warbler song, **b.** Canada Warbler call, **c.** Canada Warbler Song, **d.** Mourning Warbler call, **e.** Northern Waterthrush song, **f.** Tennessee Warbler Song

Blackpoll Warbler (*Setophaga striata*). (Figure 1a.)

A total of six vocalization detections were identified as Blackpoll Warbler, with a mean confidence score of 0.455 (SD = 0.108), ranging from 0.312 to 0.538. These detections occurred across three different days: January 14, January 15, and January 27. Furthermore, I manually found a total of 9 vocalizations and measured their acoustic structure (Table 1). All were emitted in the morning, with start times recorded at 6:34, 8:06, and 6:48. The vocalizations consisted exclusively of “rapid trills” (Bent, 1953; Brand, 1938; DeLuca *et al*., 2020; Harrison, 1986), with a rate of 10 to 12 songs per minute and an average of 13 to 20 notes per song. All detections occurred in edge habitats or open field areas in the Arrierito Antioqueño reserve. False positives included only Ash-browed Spinetail (*Cranioleuca curtata*), but this species has a variable cadence and a decreasing frequency.

Canada Warbler (*Cardellina canadensis*). (Figure 1b. 1c.) For the AAM all individuals recorded were moving constantly high in the canopy doing calls, individuals were adults of both sexes (2 males, 1 female). They were all taken in the morning (6:32-7:39), and in two different days (February 6 and 10).

For PAM, a total of 52 vocalization detections were identified as Canada Warbler, with a mean confidence score of 0.5306 (SD = 0.173), ranging from 0.315 to 0.940. Vocal activity was recorded on nine different days: January 13 and 14, and February 2, 3, 4, 5, 6, 8, and 16. Vocalizations occurred during both morning and afternoon hours, with start times as early as 6:05 and 16:12. After manual review, I found two vocalization types: songs and calls (Demko *et al*., 2013; Reitsma *et al*., 2020; Spector, 1992). I found and analyzed a total of 105 calls and 31 songs and measured their acoustic structure (Table 1). Detected call sessions exhibited considerable variation, with call rates ranging from 35 to 65 calls per minute and individual sessions containing between 7 and 63 calls (mean=20.89, SD=16.62). Song phrases consisted of 2 to 10 notes each, grouped into 7 to 27 phrases per session.

Vocal activity occurred across multiple habitats, including forest edges, interior forest, and shaded coffee plantations in both the Arrierito Antioqueño and Reinita Cielo Azul reserves. While the overall acoustic profile was consistent, a source of false positives given by BirdNET was the Three-striped Warbler (*Basileuterus tristriatus*), which can be distinguished by its more irregular cadence and higher frequency calls.

Mourning Warbler (*Geothlypis philadelphia*). (Figure 1d.) For the AAM, all individuals recorded were hopping near the ground in borders and thickets doing calls; individuals were adults of both sexes (3 males, 1 female). They were recorded in the morning (6:32-7:39) and the afternoon (16:41), and on two different days (February 6 and 7).

A total of 85 vocalization detections were identified as Mourning Warbler, with a mean confidence score of 0.515 (SD = 0.169), ranging from 0.302 to 0.931. Vocal activity was recorded on February 3, 5, 6, 7, and 9, occurring during both early morning (6:10–7:27) and afternoon (16:10–17:46) hours. Call rates within vocal bouts ranged from 20 to 49 calls per minute (mean=34.63, SD=9.81), with individual sessions containing between 19 and 74 calls (mean=42.83, SD=20.04). Manually annotated recordings showed exclusively tshrip calls (Cox, 1960; Pitocchelli, 2020). I found and analyzed 85 confirmed calls and measured their acoustic parameters (Table 1).

These calls were emitted in border areas and shaded coffee plantations only within the Reinita Cielo Azul reserve. False positives given by BirdNET included the Blackish-blue Seedeater (*Amaurospiza moesta*) and the Indigo Bunting (*Passerina cyanea*), which produce acoustically similar calls in similar frequency bands. However, the geographic distribution of these species helps to rule them out as likely sources of confusion.

Northern Waterthrush (*Parkesia noveboracensis*). (Figure 1e.)
A total of 15 vocalization detections were identified as Northern Waterthrush, with a mean confidence score of 0.532 (SD = 0.127), ranging from 0.356 to 0.780. Vocal activity was recorded on January 15 and 27, and February 11, with start times in the morning and afternoon, at 8:10 and 18:13. Detected call rates ranged from 10 to 12 calls per minute, with sessions containing between 5 and 40 notes. The only vocalization recorded was the chink call (Brown, 1975; Whitaker & Eaton, 2020). A total of 14 manually confirmed calls were analyzed for their acoustic structure (Table 1).

These vocalizations were detected in edge habitats and near water sources in both the Arrierito Antioqueño and Reinita Cielo Azul reserves. No clear false positives were identified by the BirdNET model, and the vocal characteristics, habitat, and species distribution supported reliable identification.

Tennessee Warbler (*Leiothlypis peregrina*) (Figure 1f.)
A total of 5 vocalization detections were identified as Tennessee Warbler, with a mean confidence score of 0.467 (SD = 0.094), ranging from 0.413 to 0.633. These detections occurred on January 14, 15, and 26, only in the morning, with start times at 6:29, 6:32, and 8:06. The vocalizations consisted exclusively of “two-part songs” (Rimmer & McFarland, 2020; Spector, 1992), delivered at a rate of 9 to 14 songs per minute, with each song containing between 9 and 12 notes. A total of 16 manually confirmed songs were analyzed for acoustic parameters (Table 1).

All vocalizations were recorded in border habitats and open fields within the Arrierito Antioqueño reserve. False positives included the Slate-throated Redstart (*Myioborus miniatus*), which sings at lower frequencies; the Bananaquit (*Coereba flaveola*), which produces faster notes at higher frequencies; and the Variable Seedeater (*Sporophila schistacea*), whose songs are more complex and include a wider variety of note types.

Table 1. Mean (± SD) values of duration, mean frequency, peak frequency, and entropy measured for each species' vocalizations. The numbers in parentheses after each vocalization type represent the number of vocalizations analyzed for each type.

Vocalization (260)	Duration (s)	Mean Frequency (Hz)	Peak Frequency (Hz)	Entropy
Blackpoll Warbler Song (9)	1.156±0.152	8145.5±50.78	7958.3±127.9	2.850±0.270
Canada Warbler Call (105)	0.088±0.032	5511.1±376.28	4914.3±1209.2	3.872±0.772
Canada Warbler Song (31)	1.409±0.270	6498.6±562.73	5836.7±553.0	3.424±0.498
Mourning Warbler Call (85)	0.064±0.016	5626.9±308.37	5661.4±647.4	4.252±0.441
Northern Waterthrush Call (14)	0.093±0.025	9509.7±449.53	5357.1±477.8	3.736±0.212
Tennessee Warbler Song (16)	1.442±0.239	7732.1±283.42	6761.7±823.6	3.734±0.276

Discussion

Five New World Warblers were found to vocalize (Blackpoll Warbler, Canada Warbler, Mourning Warbler, Northern Waterthrush, and Tennessee Warbler) during their residence in wintering areas in Colombia. Vocalizations were a mix of calls and songs, and for the Canada Warbler, both. Calling and singing were made mainly in forest borders, open areas, and coffee plantations, highlighting the importance of these areas for migrant birds' arrival (Bayly *et al*., 2016; González *et al*., 2021). Start times for birds vocalizing were both in the morning and in the afternoon time periods, the same as recorded in temperate areas (Bent, 1953; Harrison, 1986; Spector, 1992). Recorded behavior showed constant calling from safe areas: canopy for Canada Warbler and thickets for Mourning Warbler (Cox, 1960; Harrison, 1986). All of which shows a wide and diverse array of vocal behavior for this species in the tropics during their migration.

The Blackpoll warbler's "rapid trill" song found has no well-defined function (DeLuca *et al*., 2020) and has only been described in wintering grounds; it has been reported as the most used song in some cases (Eliason, 1986); only males sing from high perches and use it in male-male interaction, which is similar to the Category 2 song described by (Spector, 1992). The Canada Warbler does not have stereotyped songs; instead, it uses a series of phrases in each song. Males use two singing modes (Demko *et al*., 2013). It appears that the recordings show Mode II, since it has a high rhythm variation, high song rate, and chips between phrases. Also this Mode is linked to the post-fledging stage, which may overlap with the wintering period; however, songs were produced in the morning, a timing typically associated with Mode I (Demko *et al*., 2013, 2016; Reitsma *et al*., 2020). Call notes are known to function to alert mates of potential danger and are given by both sexes (Bent, 1953; Reitsma *et al*., 2020). In breeding grounds, Mourning Warbler thsrip calls are given by both males and females when predators approach nests or territories, as well as by males during territorial fights (Cox, 1960; Pitocchelli, 2020). There is no evidence of vocalizing in wintering grounds, despite high detection and abundance recorded in Colombia. The Northern Waterthrush's chink call is used to maintain feeding territory in winter and during migration, as well as a location call (Brown, 1975; Rappole & Warner, 1976). It has been described in wintering grounds (Venezuela) (Bond, 1957; Schwartz, 1964; Skutch, 1957), where birds responded to playback of the calls. Finally, the Tennessee Warbler's "two-part song" is the least common song type for the species; only the males sing (Lemon *et al*., 1983, 1987; Spector, 1992), and it is believed to be related to the defense of breeding territories (Bent, 1953; Rimmer & McFarland, 2020). There has been evidence of Tennessee Warblers producing calls during migration in foraging contexts as well as intra- and interspecific flocking (Morton, 1980; Tramer & Kemp, 1980), but I found no evidence of that happening.

Survival during the non-breeding season depends on a bird's ability to secure resources, avoid predation, and maintain family and cooperative bonds. In this context, vocal behavior can play a key role in mediating competition, facilitating social cohesion, and potentially improving future reproductive success. There are several ecological, physiological, and behavioral explanations for why migratory birds may vocalize during the non-breeding season. From an ecological perspective, some species may defend non-breeding individuals or group territories, and vocalizations can serve to establish, maintain, or defend these areas by using alarm calls vocalized by both males and females (Morton & Stutchbury, 2012; Nocera *et al*., 2008; Sorensen, 2014; Sorensen *et al*., 2016) which is likely what happened with the Canada Warbler, Northern Waterthrush, and Mourning Warbler. Behaviorally, vocal activity during winter may also play a role in social interactions such as distinguishing between neighbors and strangers (Katti, 2001) or in recognizing familiar individuals within inter- or intraspecific flocks (Block *et al*., 2021; Nowicki, 1983). The song improvement hypothesis proposes that individuals continue to sing in winter to practice and refine songs in preparation for the breeding season (Souriau *et al*., 2019), or fledglings may have their period of vocal learning in wintering areas (Warren, 2003). Physiologically, residual levels of testosterone after migration may also contribute to continued vocal behavior

during the non-breeding period, as this enlarges vocal control regions in the brain, which results in singing behavior (Brewer *et al*., 2020; Covino *et al*., 2017; Dawson *et al*., 2001; Dloniak & Deviche, 2001). These mechanisms are not mutually exclusive nor confirmed and may interact depending on the species, age, and social context of individuals. Altogether, winter vocalizations may serve multiple functions that contribute to an individual's immediate survival and future reproductive success.

This study highlights the importance of Colombia as a critical wintering area for Nearctic-Neotropical migrants (Bayly *et al*., 2016; Gómez *et al*., 2015; González *et al*., 2021). Notably, I detected the Blackpoll Warbler, a species listed as Near Threatened (NT) by the IUCN due to long-term population declines associated with habitat loss and climate change (Birdlife International, 2018). Understanding vocal behavior in wintering grounds can aid in identifying essential habitats, estimating population presence, and improving monitoring techniques for conservation planning, especially in understudied regions like the tropics (Abrahams, 2022; Penar *et al*., 2020). Natural reserves like Arrierito Antioqueño and Reinita Cielo Azul play a fundamental role in supporting these species during a vulnerable stage of their annual cycle. For future studies, I suggest investigating the probable functions of vocal production in winter. Additional research should explore other key phases of migration in the tropics, such as arrival and departure, to better understand the temporal dynamics of vocal activity. I was able to successfully record and prove New World Warblers vocalizing in their wintering rounds in Colombia, thanks to the combination of both AAM and PAM as well as automatic detection. I was able to process more than 300 hours of continuous recording and identified five species: Blackpoll Warbler (*Setophaga striata*), Canada Warbler (*Cardellina canadensis*), Mourning Warbler (*Geothlypis philadelphia*), Northern Waterthrush (*Parkesia noveboracensis*), and Tennessee Warbler (*Leiothlypis peregrina*). I was also able to identify the type of vocalizations, measure their acoustic structure and parameters, phenology, and ecological context to have a detailed vision of their vocal behavior.

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