

**COMMUNICATION AND REPRODUCTIVE BEHAVIOUR OF THE
BERMUDA WHITE-EYED VIREO (*Vireo griseus bermudianus*) AND
OTHER VIREONIDS**

By

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Abstract

Vocal displays are one of the primary ways songbirds communicate. The drivers of bird song diversity, how it might promote speciation through reproductive isolation, and their role in mate attraction and territory defence, can be better understood by studying variation within avian families. I studied the structure and function of songs in Vireonidae, and the nesting and singing behaviour of the Bermuda White-eyed Vireo (*Vireo griseus bermudianus*). I found that Vireonidae song traits have phylogenetic signal, with song traits being more similar among closer relatives than among distant relatives. I also found that species with smaller bodies and bills produced higher peak frequencies than bigger species. Using song playback, I tested whether male Bermuda Vireos, which are allopatric to all other vireonids, perceive this song diversity and adjust their response strength according to acoustic similarity that is related to phylogenetic history. Bermuda Vireos exhibited more vocalizations and speaker interactions during playbacks of closer relatives versus distant relatives, and to songs with more acoustic similarity to Bermuda Vireos. After studying their nesting cycle, I learned that breeding pairs in this subspecies sometimes remain paired for at least four years, and that they build small, cup-shaped nests in native and introduced trees. During February – September, both sexes performed nest building ($N = 13, 5 \pm 3$ days; mean \pm SD), incubation (11, 14 ± 2 days), nestling care (6, 11 ± 2 days), and fledgling care (5, 41 ± 12 days). Nest predation from introduced predators caused most nest failures. I then quantified their song rates during these nesting stages to understand how song functions in mate attraction, territory defence, and nest predator avoidance. Despite singing year-round, males during the breeding season without nesting duties sang more than males with nesting duties. Males sang less during the nestling stage, when predation was highest. Song perch height was higher during the breeding season than the non-breeding season, among

males without nesting duties compared to males with nesting duties, and when males produced discrete songs rather than rambling songs. My doctoral thesis sheds light on factors shaping bird song structure, how receivers perceive these signals, and how males use them to communicate their breeding status and territory ownership.

General Summary

Passerines use songs to communicate with one another and their acoustic properties can vary among species. The factors that contribute to song diversity, the role of song in reducing hybridization, and how bird song functions in mate attraction and territory defence require studies on several bird species. I studied the structure and function of songs in Vireonidae, and the nesting and singing behaviour of the Bermuda White-eyed Vireo (*Vireo griseus bermudianus*). Vireonid song traits were more similar among closer relatives than among distant relatives, and species with smaller bodies and bills sang with higher peak frequencies than larger vireos. Using song playback, I tested whether male, Bermuda Vireos, whose breeding range does not overlap with any vireo relatives, perceive this song diversity and adjust their response strength to acoustic similarity, due to common ancestry. Bermuda Vireos exhibited more vocalizations and speaker interactions during playbacks of closer relatives than distant relatives, and to songs that were more similar-sounding to the songs to Bermuda Vireos. After studying their nesting cycle, I learned that this bird builds small, cup-shaped nests in native and introduced trees, and that some breeding pairs remain together for at least four years. During February – September, both sexes performed nest building ($N = 13$, 5 ± 3 days; mean \pm SD), incubation (11, 14 ± 2 days), nestling care (6, 11 ± 2 days), and fledgling care (5, 41 ± 12 days). Nest predation from introduced predators caused most nest failures. I then documented their singing behaviour during these nesting stages to understand how song functions in mate attraction, territory defence, and nest predator avoidance. Despite singing year-round, males during the breeding season without nesting duties sang more than males with nesting duties; males sang less when feeding nestlings, when predation was highest. Song perch height was higher during the breeding season versus the non-breeding season, among males without nesting

duties compared to males with nesting duties, and when males produced their primary song rather than another, less used song type. My doctoral thesis highlights factors shaping bird song structure, how birds perceive these songs, and how males use them to communicate their breeding status and territory ownership.

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List of Abbreviations and Symbols

ANOVA: Analysis of variance

B: Blue

K: Blomberg's *K*

°C: Celsius

d: Days

dB: Decibel

DBB: Depth of bill at its base

DBN: Depth of bill at the anterior margin of the naris

ddRAD: Double digest restriction-site associated DNA

ESS: Effective sample size

FFT: Fast Fourier transform

G: Green

ha: Hectares

h: hours

Hz: Hertz

in: Inches

λ : Lambda (i.e., Pagel's lambda)

LEC: Length of exposed culmen

LB: Light blue

ln: natural log transformation

LNB: Length of bill from the anterior margin of the naris to the tip

\bar{x} : Mean

m: Meters

mm: Millimeters

M. A. Mejías: Miguel Alberto Mejías

min: Minutes

MCC: Maximum clade credibility

MCMC: Markov chain Monte Carlo

μl: Microliter

μM: Micrometers

ms: Milisecond

N: Sample size

ND2: NADH dehydrogenase 2

O: Orange

pp: Posterior probability

PGLS: Phylogenetic generalized least square

pers. observ: Personal observations

pers. comm: Personal communication

P: Pink

PU: Purple

pPCA: Phylogenetic principal component analysis

R: Red

s: Seconds

SD: Standard deviation

SPL: Sound pressure level

unpubl. data: Unpublished data

VIFs: Variance inflation factors

W: White

WBB: Width of bill at its base

WBN: Width of bill at the anterior margin of the naris

Y: Yellow

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Chapter 1:
General Introduction

Introduction

Given their cosmopolitan distribution and conspicuous vocal displays, birds have intrigued amateur and professional ornithologists for centuries. Traditionally, people spoke of birds primarily from an aesthetic perspective, where their gaudy plumage and songs were referenced in art, stories, books, and mythology (Tüür 2009). In time, our bird obsessions lead to intriguing questions about how their existence came to be and would eventually serve as one of the pillars to biological and behavioural sciences. For example, the 20th century marked the birth of bioacoustics, bringing to light the diverse nature and complexity of avian vocal behaviour (Thorpe 1961, Morton 1977, Kroodsma and Miller 1996). It is because of bioacoustics that we now recognize that songs (typically long, complex signals) and calls (often short, simple signals) can have distinct functions (Catchpole and Slater 2003). Songs are thought to be important for mate attraction, territory defense, and stimulating breeding behaviour (Krebs et al. 1978, Searcy and Anderson 1986, Catchpole 1987, Logan et al. 1990, Kroodsma and Byers 1991). Bird calls are used for maintaining flock formation, signaling threat presence and the discovery of food, and alerting the whereabouts between mates (Barlow and Rice 1977, James 1984, Kumar 2003, Farnsworth and Lovette 2008). Bird song structure varies greatly across taxa, despite serving the same functions. Indeed, it is this diversity in acoustic structure that drives robust hypothesis testing in behavioural ecology, which is fundamental to understanding how important these signals are to the evolution and maintenance of avian speciation and sociality.

In this doctoral thesis, I describe the natural history of a poorly-known island endemic subspecies, the Bermuda White-eyed Vireo (*Vireo griseus bermudianus*), and then use this species and its relatives to advance our understanding of the evolution, structure, and function of song. Members of the Vireonidae are vociferous, with species showing remarkable song

diversity within and among genera. Of the eight recognized genera (Brewer et al. 2019), songs belonging to the *Vireo* genus have received the most study, particularly in North America (Borror 1981, Borror 1987, Hedley 2016, Lovell et al. 2021). Slager et al. (2014) published the most comprehensive phylogenetic tree for Vireonidae to date, depicting the relationships among 50 of the 64 recognized species. This phylogeny opens additional avenues of research and analyses. First, this phylogenetic tree allows me to test, for the first time, whether common ancestry predicts the acoustic structure of vireonid songs, and to control for phylogenetic relationships while testing the effects of habitat type and morphology on song structure. Second, I can explore phylogenetic relationships by adding lesser known vireonids to the Slager et al. (2014) tree, like the Bermuda White-eyed Vireo. Due to allopatry, this subspecies is largely naïve to the songs of all other Vireonidae, allowing me to test whether phylogenetic distance between the Bermuda White-eyed Vireo and stimulus species predicted response strength to song playback, and if acoustic similarity between the former and one of its vireonid relatives was the mechanism for adjusting response strength. Its allopatry with family members is important in removing the confounding factors imposed by signal familiarity, thus permitting me to test directly the underlying mechanisms of avian song perception, which could ultimately drive speciation. While we as researchers often emphasize the importance of bird song in mate attraction, ironically, the actual nesting behaviour of our study organism(s) is sometimes unknown; this is the case with the Bermuda White-eyed Vireo. Studying this subspecies' nesting cycle and the threats it faces throughout its breeding season ultimately enabled me to test specific hypotheses about when and where males sing throughout the breeding stages.

Phylogenetic history and bird song structure

In *On the Origin of Species*, Darwin (1859) explained that all species within a genus, as well as those within higher taxonomic levels, must be descendants from common ancestors, the latter passing on heritable traits to the former across generations. It is here where the foundation of descent with modification lies, with structural similarity typically occurring among closely related species (Gregory 2008). Using phylogenetic trees, researchers have developed a metric of phylogenetic trait similarity called phylogenetic signal, where larger values reflect higher trait similarity resulting from close phylogenetic relationships, compared to pairwise comparisons among species drawn at random from the same tree (Pagel 1999, Blomberg et al. 2003, Laiolo and Rolando 2003). Phylogenetic signal is often tested on morphological traits, as seen in plants (Fougère-Danezan et al. 2010, Roncal et al. 2012), birds (Puga-Caballero et al. 2020, Zhou et al. 2021), mammals (Gamarra et al. 2016, Hulme-Beama et al. 2019), insects (Chursina and Negrobov 2018, Karthika et al. 2021), and reptiles (Ashton and Feldman 2003, Gentilli et al. 2009). Given its prevalence in morphological traits, it seems plausible that bird song traits might also exhibit phylogenetic signal. Despite significant phylogenetic signal being found in the song traits of some avian species such as kinglets (Regulidae; Päckert et al. 2003), doves (Columbidae; de Kort et al. 2001), warblers (Phylloscopidae; Tietze et al. 2015), and wrens (Troglodytidae; Sosa-López et al. 2016), phylogenetic signal in song remains unexplored in many avian families. Thus, it is still unclear how ubiquitous phylogenetic history is in shaping avian song structure.

Habitat and bird song structure

Habitat structure is also hypothesized to be an important factor in shaping bird song structure for optimal signal transmission. More specifically, the acoustic adaption hypothesis

predicts that temporal and frequency traits of bird songs are influenced by differences in the number of sound-reflecting surfaces, such as trees, in avian habitats (Morton 1975). In line with Morton's predictions, several researchers have found that songbirds living in dense forests (i.e., closed habitats) tend to sing shorter songs with narrower frequency ranges, lower frequencies, and larger silent gaps between elements, whereas songbirds living in grasslands and shrublands (i.e., open habitats) tend to sing longer songs with broader frequency ranges, higher frequencies, and smaller silent gaps (Morton 1975, Sorjonen 1986, Van Dongen and Mulder 2006, Barker 2008). The mechanics of this observed pattern can best be explained by higher frequency sounds having wavelengths smaller than the diameter of the trees, and when these short wavelengths hit a tree, they are more likely than long wavelength sounds to be reflected. In contrast, a long wavelength sound is larger than most objects it hits, so is more likely to pass by trees without being reflected or distorted. As a result, in forested habitats, short, tonal songs travel farther, with less reverberation, than longer songs with higher frequencies (Morton 1975, Barker 2008). Results of the acoustic adaption hypothesis, however, are mixed (Ey and Fischer 2009). Therefore, testing this hypothesis among additional avian families is necessary for improving our understanding of avian song evolution.

Morphology and bird song structure

Bill shape and body size are two important traits that are known to affect bird vocalizations. Although natural selection has improved survival of avian species by modifying heritable morphological traits like bill size for optimal handling of specific food items (Grant and Grant 1996), such changes have simultaneously affected the acoustic properties of the singer. Generally, birds with larger bills cannot open and close their bills as fast as songbirds with smaller bills. Since opening and closing the bill modulates the frequency components and rate at

which elements are produced in bird songs, the size of the bill, and thus the maximum rate at which it can be opened and closed, can constrain the degree of frequency modulation and speed of element delivery that is possible (Ryan and Brenowitz 1985, Palacios and Tubaro 2000). Body size, however, is related to the size of the syringeal membrane, which affects the minimum frequencies that can be produced in bird vocalizations (Wallschläger 1980). Compared to smaller birds, larger birds tend to sing songs with lower frequency ranges and (Wallschläger 1980, Ryan and Brenowitz 1985,). As with phylogeny and habitat, the potential effects of bill or body size on song structure have yet to be tested in many avian families.

Effects of phylogenetic history and acoustic structure on avian song perception

For avian speciation to occur, not only do species signals need to change, but recipients' responses to those signals must diverge accordingly (Marler 1957, Nelson and Marler 1989). For example, selection should act on female preferences to respond most strongly to conspecific male song, whilst ignoring male congeneric song (Kirschel et al. 2009, Seddon and Tobias 2010). Since song is essential for attracting mates and defending territories, such divergence in songs and song perception presumably leads to reproductive isolation among closely related species, resulting in speciation (Hansen 1978, Kumar 2003, Patten et al. 2004). Although researchers acknowledge that bird song structure exhibits phylogenetic signal, there are only a few studies that have explored whether birds perceive and adjust their responses to foreign signals according to phylogenetically conserved traits; this is especially true for species that are allopatric to their closest relatives (de Kort and ten Cate 2001, Sosa-López et al. 2016). Under allopatry, closely related species never interact, which removes signal familiarity as a factor driving signal perception (de Kort and ten Cate 2001, Ryan et al. 2003). Therefore, responses to congeneric song by a species that is allopatric with congeneric species are likely due to acoustic

similarity among their songs due to phylogenetic relatedness (Sosa-López et al. 2016), though more studies of this nature are needed to garner stronger support of this hypothesis.

Temporal and social factors on singing rate and song perch height in songbirds

Bird song is hypothesized to be important for mate attraction and territory defence (Kroodsma and Byers 1991). This is arguably most pronounced in neotropical migrant songbirds that sing prolifically on their breeding grounds in spring and summer, and then cease singing in fall and winter. Migrant songbirds presumably stop singing on wintering grounds because they no longer need to attract mates or defend breeding territories; breeding pairs in the tropics, in contrast, remain together year-round and use song to constantly defend territories (Diamond 1974, Slater and Mann 2004). In North America, researchers have tested the importance of bird song by comparing the singing rates of males that are either paired or unpaired with females, with the general prediction being that paired males would sing significantly less than unpaired males. To date, some evidence congruent with this pattern has been found in several continental breeding populations of vireos (James 1983, Howes-Jones 1985), New World warblers (Parulidae; Staicer et al. 2006, MacDonald and Islam 2021), and wrens (Troglodytidae; Rendall and Kaluthota 2013, Kaluthota et al. 2020). Among continental breeders, studies have also found that male singing rate declines as male songbirds cycle through courtship, nest building, incubation, and chick rearing (Gil et al. 1999, Bolsinger 2000, Liu and Kroodsma 2007). One possible explanation for this pattern is that singing may alert predators to bird nests, with predation risk hypothesized to be higher during nestling care compared to the egg stage (Morton et al. 1993). Most studies of this nature, however, are on neotropical migrants, whereas the effects of season and nesting status in male singing behaviour is seldom studied on non-migratory passerines.

Even fewer studies have focused on the effects of mating status on song perch choice, despite anecdotal evidence of male songbirds using higher song perches during the breeding season (Castrale 1983, Rodenhouse and Best 1983). It is possible that bachelor males use higher song perches to make themselves more visually conspicuous to prospecting females (Fernández-Juricic et al. 2005, Jones and Islam 2006, Hallworth et al. 2008). One of the best demonstrations of this pattern was seen in Chipping Sparrows (*Spizella passerine*) in Massachusetts, where unpaired males sang from the highest song perches, but stopped singing atop high perches once paired with a female (Liu and Kroodsma 2007). Identifying preferred song perches can provide crucial contextual information for understanding song function (Upham-Mills et al. 2020). At present, however, too few studies have tested for relationships between male pairing status and song perch height, which makes assessing the ubiquity of this behaviour among songbird species difficult to interpret.

The genus Vireonidae

My doctoral research focuses on the vocal displays in the Vireonidae. Eight recognized genera currently compose the family: *Pteruthius* and *Erpornis* are only found in southern and eastern Asia, whereas *Vireo*, *Hylophilus*, *Pachysylvia*, *Tunchiornis*, *Cyclarhis*, and *Vireolanius* are endemic to the Western Hemisphere, with a cumulative distribution from Alaska, southward throughout North America, to the islands of Bermuda, the Caribbean, and Fernando de Noronha, and finally to Paraguay in South America (Brewer et al. 2019). All members are characterized by black and/or blueish hook-tipped bills, which are used to consume insects, spiders, lizards, and fruits (Brewer et al. 2019, M. Mejías pers. obs.). Their plumage colours exhibit different shades of greens, blues, yellows, and greys, with green usually dominating plumage colour. The word “vireo,” translates to “*I am green.*” (Brewer et al. 2019). Vireonidae are an ideal family to test

hypotheses pertaining to the evolution, structure, and function of avian song structure for several reasons. First, Slager et al's. (2014) phylogeny depicts the evolutionary relationships among most vireonids, providing the phylogenetic framework necessary to trace the history of the diverse songs sung across species. Second, vireonid species occupy a diverse array of habitats that vary in vegetation thickness, from open grasslands to dense boreal forests. Similarly, species show considerable variation in bill and body size. Third, some species are allopatric with all their family members, making them ideal candidates for investigating how phylogenetic history and acoustic structure affect song perception. Lastly, the breeding biology of some vireonids are unknown; shedding light on their breeding phenology will aid in testing hypotheses about how temporal and social factors affect male singing rate and song perch choice.

Bermuda White-eyed Vireo (Vireo griseus bermudianus)

The focal vireonid of my doctoral thesis is the Bermuda White-eyed Vireo, which is an endemic subspecies of the White-eyed Vireo found only in my home country of Bermuda (Figure 1.1). It is common across woodlands, thickets, mangroves, and gardens throughout the archipelago (Amos 1991). The loud, complex song of males can be heard year-round; a local rendition of this tune has fondly earned it the nickname “*chick-of-the-village*.” Typical of birds living on remote oceanic islands, the Bermuda White-eyed Vireo is extremely brazen and tame towards humans (Reid 1877). It is currently the only terrestrial endemic species of breeding bird that lives on the island, making it of local conservation importance. Prior to my dissertation, several aspects of the phylogeny and behaviour of this endemic, subspecies were unknown. For example, despite it being recognized as a subspecies of the continental White-eyed Vireo (Bangs 1901), its phylogenetic position had never been determined. It is also allopatric with other vireonids, making it a good candidate to test whether phylogenetic history and acoustic structure

affect responses to the songs of other species from within the respondent's family. Despite centuries-long accounts of its island-wide abundance and boldness, its breeding behaviour and phenology remained unknown. Not only will data on nesting phenology help guide conservation management decisions for the island's last endemic landbird, but it is fundamental in allowing me to test how season and breeding status affect the singing rate of male songbirds.

Thesis overview

In this PhD thesis, I explore the potential drivers responsible for song variation across the Vireonidae, I test how an allopatric vireonid perceives and responds to this song variation, I describe the breeding phenology and behaviour of a previously unstudied vireonid subspecies, and I then test how male singing behaviour in this subspecies changes with season and breeding status. More specifically, in Chapter 2, I use a phylogenetic framework to measure phylogenetic signal in vireonid song traits, as well as test whether habitat structure and morphology are related to song structure, after controlling for phylogeny. This chapter is published in *Evolution* (Mejías et al. 2020). In Chapter 3, I conduct a song playback experiment with colour-ringed Bermuda White-eyed Vireo males to test whether song traits affect the strength of behavioural responses to the songs of closer and distant vireonid relatives. I published this chapter in *The Journal of Field Ornithology* (Mejías et al. 2021). In Chapter 4, I describe, for the first time, the breeding behaviour and phenology of the Bermuda White-eyed Vireo across the entire nesting cycle. I will submit this chapter for consideration for publication in a peer-reviewed journal. In Chapter 5, I record the singing behaviour of colour-banded male Bermuda White-eyed Vireos throughout the breeding and non-breeding season and test whether their singing rate changes as a function of season, pairing status, and nesting stage. I also test if song perch height varies in relation to the breeding status of males or the song types they sing. I will submit Chapter 5 to a peer-reviewed

journal for consideration for publication. The results of this thesis derive from observational and experimental research on wild birds in the field, from analysis of the morphology of museum specimens, and from the analysis of songs from online song libraries.

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Figures



Figure 1.1. A Bermuda White-eyed Vireo feeding on what appears to be a small arachnid among the foliage of a Brazil peppertree (*Schinus terebinthifolia*). Adults are readily recognized by their bright white iris, yellow patches around the eyes and on the flanks, black legs and feet, greyish head, and two whitish wingbars. Photograph by Richard Brewer.

Co-authorship Statement

I, Miguel Alberto Mejías, hereby declare that I am the primary contributor to this doctoral thesis; its ultimate completion required invaluable, collaborative work from local and overseas researchers. In general, I took the lead on formulating research topics (alongside my supervisor, David Wilson), collecting songs from online sound libraries, colour-banding, recording, and observing vireos in the field (with the help of my parents and friends), analyzing song and breeding data (with the help of David Wilson and several student colleagues), interpreting the data, and writing all thesis chapters, each of which I am the primary author. Specific contributions, per chapter, are detailed below.

I am the sole author of Chapter 1 (General Introduction) and Chapter 6 (General Discussion). Both chapters were outlined and written by me. David Wilson provided minor edits which improved the presentation of these bookend chapters.

I am the primary author of Chapter 2, which was coauthored by Julissa Roncal, Tyler Imfeld, Sander Boisen, and David Wilson. I collected song recordings from online sound libraries, wrote the entire manuscript, and produced figures, all of which were edited by all coauthors. My supervisor proposed the research topic and wrote R code to extract annotated bird songs from song recordings. Julissa Roncal helped acquire the vireonid sequence data and suggested the appropriate phylogenetic analysis. Tyler Imfeld provided morphological data and, alongside Sander Boisen, wrote the code for statistical analysis. Chapter 2 was peer-reviewed and published: **Mejías, M. A., J. Roncal, T. S. Imfeld, S. Boisen, and D. R. Wilson.** 2020. Relationships of song structure to phylogenetic history, habitat, and morphology in the vireos, greenlets, and allies (Passeriformes: Vireonidae). *Evolution* 74: 2494–2511.

I am the primary author of Chapter 3, which was coauthored by Julissa Roncal and David Wilson. I conducted the fieldwork (with the help of my parents), quantified data from field recordings, wrote the entire manuscript, and produced figures, all of which were edited by all coauthors. David Wilson and I came up with the research topic; all three authors contributed to the experimental design. Julissa Roncal and I extracted and sequenced Bermuda Vireo's DNA, which was funded with her research grant (NSERC Discovery Grant # RGPIN-2014-03976). David Wilson helped with statistical analysis and provided field equipment needed to record singing behaviour of the Bermuda Vireo, which was funded by his research grant (NSERC Discovery Grant # RGPIN-2015-0376). Chapter 3 was peer-reviewed and published: **Mejías, M. A. and D. R. Wilson.** 2021. Territorial responses of Bermuda White-eyed Vireos (*Vireo griseus* subsp. *bermudianus*) reflect phylogenetic similarity of the intruder and acoustic similarity of its song. *Journal of Field Ornithology* 92: 431–449.

I am the primary author of Chapter 4, which I coauthored with David Wilson. I came up with the research idea, did all the fieldwork (with the help of my parents), summarized and quantified the data, wrote the entire manuscript, and produced all figures. David Wilson provided feedback which improved the manuscript. This chapter will be submitted for peer-review for future publication.

I am the primary author of Chapter 5, which I coauthored with David Wilson. I developed the key ideas, did all the fieldwork (with the help of my parents), analyze the data (with the help of David Wilson), wrote the entire manuscript, and produced all figures. David Wilson revised earlier drafts of the manuscript and provided field equipment that was funded by his research grant (NSERC Discovery Grant # RGPIN-2015-0376). This chapter will be submitted for peer-review for future publication.

Chapter 2:
**Relationships of song structure to phylogenetic history, habitat, and
morphology in the vireos, greenlets, and allies (Passeriformes: Vireonidae)***

**This Chapter (Mejías et al. 2020) is the outcome of joint research with J. Roncal, T. Imfeld, S. Boisen, and D. Wilson*

Abstract – Acoustic signals show immense variation among passerines, and several hypotheses have been proposed to explain this diversity. In this study, I tested, for the first time, the relationships of song structure to phylogeny, habitat type, and morphology in the vireos and allies (Vireonidae). Every measure of song structure considered in this study had moderate and significant phylogenetic signal. Furthermore, two song-constraining morphological traits, bill shape and body mass, also exhibited significant phylogenetic signal. Song length showed the largest within-clade similarity; longer songs were highly conserved in part of the greenlet (*Hylophilus*) clade, whereas shorter songs characterized the remaining seven genera. I found no differences in song structure among vireonids living in different habitat types. However, vireonids with shorter, stouter bills and larger bodies sang songs with lower minimum and maximum peak frequency, compared with species with longer, thinner bills and smaller bodies. I conclude that Vireonidae song evolution is driven partially by phylogenetically conserved morphological traits. Our findings failed to support the habitat (or acoustic adaptation) hypothesis, but supported the phylogenetic signal and morphological constraints hypotheses explaining structural diversity in avian acoustic signals.

Introduction

Across the globe, passerines emit both simple and complex vocal displays in multiple contexts (Kroodsma and Byers 1991, Williams 2004). Specific functions of bird song include species recognition (Falls and Brooks 1975, Kumar 2003), mate attraction (Eriksson and Wallin 1986, Searcy and Johnson 1996, Demko and Mennill 2018), territory defense (Krebs 1977, Searcy et al. 1998, Hyman 2003), and status signaling (Staicer et al. 2006, Liu and Kroodsma 2007). Although song serves these same functions in many passerines, song structure varies greatly among species (Brenowitz et al. 1997). Structural diversity in song is thought to serve as a precopulatory mechanism of reproductive isolation at species boundaries, which facilitates conspecific mating (Kreutzer and Vallet 1991, Grant and Grant 1996), reduces hybridization (Qvarnström et al. 2006, Mason et al. 2017), and, ultimately, drives speciation (Slabbekoorn and Smith 2002). By exploring the processes shaping avian song structure, we can better understand the evolution of animal signals and the roles those signals play in speciation and maintaining biological diversity.

Several non-mutually exclusive mechanisms have been proposed to explain structural variation in avian song. First, the sexual selection hypothesis (Darwin 1896, Andersson 1994, Catchpole 1980, Searcy and Anderson 1986) views song as an acoustic equivalent of a peacock's "tail", with its underlying processes, such as mate choice, driving trait elaboration (Buchanan and Catchpole 1997, Byers and Kroodsma 2009). Despite being a widely accepted mechanism, the role of sexual selection in shaping acoustic traits is challenging to quantify because data on several proxies of sexual selection, including plumage dichromatism (Seddon et al. 2008, Kraaijeveld et al. 2011; but see Price 2019), mating system (Møller and Cuervo 1998), and nesting data (Krakauer 2008, Balenger et al. 2009), are not readily available for all species. A

second driver of song structure complexity is the number of singing, sympatric heterospecifics. More specifically, conspecifics living in depauperate songbird communities have fewer acoustic competitors, facilitating selection for elaborate song structure, whereas conspecifics living amongst diverse avifauna are more restricted in their vocal diversity because of increased competition for “acoustic space” (Naugler and Ratcliffe 1994, Espmark 1999). Anthropogenic noise can have a similar effect on avian songs, with birds living in noise polluted areas exhibiting significant shifts in song frequencies, as compared to conspecifics living in areas without anthropogenic noise (Slabbekoorn and Ripmeester 2008, Hanna et al. 2011). Third, song evolution can be affected by song learning, since copying mistakes by young birds can cause “cultural drift” (Podos et al. 2004, Koetz et al. 2007). In the current study, however, I focus on three non-mutually exclusive hypotheses shaping avian song structure: (1) phylogenetic history, (2) habitat structure, and (3) morphology.

Traits that exhibit high similarity amongst closely related species, as compared to species drawn at random from the same phylogenetic tree, are said to exhibit phylogenetic signal — a pattern of trait distribution that is expected under a random walk model (Brownian motion) of trait evolution (Blomberg and Garland 2002, Blomberg et al. 2003, Münkemüller et al. 2012). With respect to bird song, closely related species have had less time to diverge and could therefore sound similar, whereas distantly related species have had more time to diverge and could sound different. Evidence of phylogenetic signal in song structure has been found in oropendolas (Icteridae; Price and Lanyon 2002), kinglets and crests (Regulidae; Päckert et al. 2003), and wrens (Troglodytidae; Sosa-López et al. 2016). In contrast, some signals may diverge more rapidly among closely related species living in sympatry than among more distantly related species living in allopatry, giving rise to an inverse relationship between phylogenetic

relatedness and trait divergence (Martin et al. 2010, 2015). Traits might also evolve rapidly to show homoplasy across the phylogeny, or even exhibit no change at all, leading to low levels of phylogenetic signal (Blomberg et al. 2003, Kamilar and Cooper 2013). Nonetheless, phylogenetic signal remains to be quantified in most avian song traits, and, thus, its prevalence in most avian families remains unclear.

Bird song can travel long distances and the quality of these vocal displays can be impacted by the physical properties of their surroundings (Morton 1975, Wiley 1991, Barker 2008). Specific habitat-induced changes to songs include sound-reflecting surfaces distorting timing between elements via echoes and reverberations, as well as absorption and scattering of frequency components by vegetation (Wiley 1991, Naguib 2003, Padgham 2004). Thus, different habitats have different acoustic properties, meaning a habitat can shape song structure by determining which songs maintain their structure (and thus, communicative value) as they propagate through the environment. In forests, for example, selection may favour birds that sing songs with lower frequencies, whereas in open habitats, selection may favour birds that sing songs with higher frequencies. For example, high-frequency sounds have wavelengths that are shorter than the diameter of tree trunks and are thus distorted and scattered as they propagate through a forest, whereas low-frequency sounds have wavelengths longer than the diameter of tree trunks and thus pass these structures and reach their intended receivers with minimal reflection or distortion (Naguib 2003). Similarly, denser habitats can select for songs with less frequency modulation, whereas open habitats can select for songs with more frequency modulation (Nemeth et al. 2001, Barker 2008). Lastly, the potential of vegetation to distort the onset and offset of individual song elements through reverberation may favour songs with fewer

elements, and reduced overall song length in forested environments, as compared to open environments (Hunter and Krebs 1979; but see Ey and Fischer, 2009).

The evolution of avian song structure can also be constrained by morphology (Podos 2001). Opening and closing the bill contributes to a song's frequency modulation (Ryan and Brenowitz 1985, Palacios and Tubaro 2000), but species with larger bills cannot open and close their bills as fast as species with smaller bills while singing (Ballentine 2006). Natural selection for the large bills needed to handle hard food items could thus lead to songs with little frequency modulation, whereas selection for the long, thin bills needed for capturing insects could lead to songs with rapid frequency modulation (Herrel et al. 2005, Huber and Podos 2006). Bill shape can also impact the rate of element delivery within songs, with larger bills uttering elements at a slower rate (Huber and Podos 2006, Derryberry et al. 2012), although the effects of bill morphology on other temporal traits, like song length, are not well established. The size of the syrinx also covaries with body size (Bowman 1979); the larger syrinx of a larger species should thus vibrate slower and produce sounds of lower frequency (Wallschläger 1980) than the smaller syrinx of a smaller species (Bowman 1979, Ryan and Brenowitz 1985, Nowicki and Marler 1988). Larger birds also experience greater respiratory constraints than smaller birds (Suthers 2001) and may thus produce shorter songs.

Vireonidae is a diverse avian family ideal for testing multiple hypotheses of song evolution. First, a recent multilocus phylogenetic study containing 50 of the 64 recognized species showed a monophyletic Vireonidae (Slager et al. 2014). The family comprises eight genera: *Pteruthius* and *Erpornis* are endemic to southern and eastern Asia, and the remaining six genera (*Vireo*, *Hylophilus*, *Pachysylvia*, *Tunchiornis*, *Cyclarhis*, and *Vireolanus*) are endemic to the New World, ranging from Alaska to forests of the Caribbean, Bermuda, and South America

(Slager et al. 2014, Brewer et al. 2019). Second, vireonids occupy diverse habitat, including shrublands, thickets, woodland edges, and the interior of temperate and tropical forests (Barlow and James 1975, Kus 1998, Hudman and Chandler 2002). Third, species vary dramatically in bill structure and body size (6-35 g; Brewer et al. 2019), and fourth, vireonids exhibit substantial variation in song structure, including duration, the minimum and maximum song frequencies, and frequency modulation. Vireonid songs are also unusual in that this family dispersed out of Asia (Slager et al. 2014) into the Western Hemisphere independently from the Australasian-derived Passerida (Barker et al. 2004), yet some vireonids sing songs more like New World passerines, such as Passerellidae and Troglodytidae, as opposed to the less complex songs of their closer relatives in Corvoidea.

My objective was to test for relationships of vireonid song structure to phylogenetic history, habitat structure, and morphology. First, I tested for phylogenetic signal in Vireonidae song traits; upon finding significant phylogenetic signal in vireonid songs, I measured phylogenetic signal in bill shape and body size. This was important because phylogenetic history might also shape these potential song-constraining traits, ultimately driving song trait distribution in Vireonidae. As with phylogenetic signal in song structure, I predicted that more closely related species would have greater similarity in bill shape and body size, as compared to more distantly related species. Having detected phylogenetic signal in song traits, I then performed a series of phylogenetically informed analyses to test for relationships between vireonid song structure and habitat type, bill shape, and body size. I predicted that vireonids living in dense habitats would sing shorter songs, with lower minimum and maximum frequencies, and less frequency modulation. In contrast, I predicted that vireonids living in more open habitats would sing longer songs, with broader frequency ranges, and more frequency modulation. Finally, I predicted

inverse relationships between morphology and song traits; specifically, species with deeper, larger bills would sing shorter songs with smaller frequency ranges and less frequency modulation, as compared to species with smaller, thinner bills. Similarly, I expected larger-bodied vireonids to sing shorter songs with narrower frequency ranges and less frequency modulation, and smaller-bodied vireonids to sing longer songs, with broader frequency ranges and more frequency modulation.

Methods

Phylogenetic inference

Slager et al. (2014) inferred the evolutionary relationships among 50 (78%) of the 64 currently recognized species in the Vireonidae (Brewer et al. 2019). Their phylogenetic analyses based on the mitochondrial ND2 locus and three Z-linked nuclear loci showed that the North American and South American Red-eyed Vireo (*Vireo olivaceus*) represent two divergent lineages, suggesting two distinct species. Battey and Klicka (2017) further explored this relationship with ddRAD sequencing and concluded that the two are not sister taxa, and do not exchange genes. They recommended elevating the South American lineage to species status under its original name, Chivi Vireo (*V. chivi*; Vieillot 1817), leaving the North American lineage as *V. olivaceus*; I thus treat *V. chivi* and *V. olivaceus* as separate species, and follow the nomenclature of the American Ornithological Society (Chesser 2019) for the other species. Therefore, I recognize 51 species on the phylogenetic tree of Slager et al. (2014).

I obtained the mitochondrial ND2 alignment from Slager et al. (2014). It contained the most comprehensive taxonomic sampling for Vireonidae, including multiple individuals per

species (Figure 1 in Slager et al. 2014). Sampling for the three Z-linked nuclear loci was poor (52%), and thus these loci were not used in my study. Since the multispecies coalescent model cannot be used reliably with a single gene dataset to infer a phylogenetic tree that will include one representative per species, I selected the longest ND2 sequence per species, or randomly selected one when they had equal lengths and completeness. My resulting ND2 alignment contained 51 of 64 (80%) vireonids; *Pteruthius*, *Erpornis*, and *Cyanocitta* were included as outgroups, as in Slager et al. (2014).

I used the Bayesian method implemented in BEAST v2.5.2 (Bouckaert et al. 2014), and the parameters described in Slager et al. (2014) for the codon partitions, substitution site model, tree prior, and clock model. I enforced the monophyly of the Vireonidae genera using a series of taxon sets to obtain a tree with the same relationships as in Slager et al. (2014). I used a single run of a Markov chain Monte Carlo (MCMC) chain length of 150 million generations on the CIPRES Science Gateway (Miller et al. 2010), sampling trees every 150 thousand generations, producing a file with 1000 trees, and a log file with the respective posterior probabilities (pp) per tree. I sampled all other parameters every 15 thousand generations. I verified that the MCMC run reached convergence by viewing the output in Tracer v1.7 (Rambaut et al. 2018), and that all effective sample sizes exceeded 200. Following the removal of 25% burn-in, the remaining 750 sampled posterior trees were summarized using Tree Annotator v.2.5.2 (Bouckaert et al. 2014) to generate a maximum clade credibility tree (hereafter, “MCC Vireonidae tree”) and calculate the pp as branch support values. I visualized the Bayesian inference tree in FigTree v.1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Habitat classifications

Many life-history and behavioural data are scant for vireonids outside of North America. Due to this limitation, I utilized a three-way habitat categorization; this methodology was adopted in previous studies (Tubaro and Segura 1995, Mason and Burns 2015). For each species, I used habitat descriptions from the Handbook of the Birds of the World (Brewer et al. 2019) to group it into one of three broad habitat categories, from closed to open: (1) woodlands, (2) open woodlands, or (3) shrublands. Woodland habitat is forest with a dense interior and a dense understory (Morton 1975, Brewer et al. 2019). Open woodland is a forest with gaps in its interior, either from clear cutting or tree fell, and little to no understory (Brewer et al. 2019). Shrubland is grassland covered with extensive saplings and shrubs, interspersed with scattered larger trees and bushes (Brewer et al. 2019). Morton (1975) described some tropical vireonids inhabiting edge or canopy habitats. He considered edge habitat to be intermediate between forest and grassland, and canopy habitats to be less open than edge habitat. Therefore, I categorized edge-dwelling species in open woodland habitat and canopy-dwelling vireonids in woodland habitat.

Body measurements

Two morphological variables were quantified from vireonids: (1) bill shape and (2) body mass. Bills were measured from specimens from the following collections: The Field Museum, American Museum of Natural History, Museum of Natural Science at Louisiana State University, and the Bell Museum at the University of Minnesota (Table 2.S1). A digital caliper (Mitutoyo® model no. 573-721) was used to measure (± 0.01 mm) the following variables on the bill (Baldwin et al. 1931): (1) length of exposed culmen (LEC), (2) length of bill from the anterior margin of the naris to the tip (LNB), (3) width of bill at its base (WBB), (4) width of bill

at the anterior margin of the naris (WBN), (5) depth of bill at its base (DBB), and (6) depth of bill at the anterior margin of the naris (DBN). When possible, three males from the same breeding population were measured. If three males that met these criteria were not available, specimens were measured that matched, in declining priority, subspecies, locality, and time of year. Female specimens were measured only when three males that met my criteria were not available, but no more than one female specimen was measured per species. When fewer than three specimens meeting any of these criteria were available, all available specimens were measured. Specimens of the Chivi Vireo were not measured because it had not been elevated to species at the time of data collection; instead, I included data on three bill measurements (LEC, WBB, and DBB) for Chivi Vireo from Olson (1994). I estimated the three missing bill measurements by regressing the missing variables against their complements (e.g. LBN ~ LEC) and using the slope and intercept to estimate means for the missing variables. I collected body mass data from the VertNet Museum Database (<http://vertnet.org/>) and the Handbook of Birds of the World (Brewer et al. 2019). For each species, I calculated mean values for each bill measurement and body mass and improved data normality by ln-transforming means prior to phylogenetic comparative analysis (Safi et al. 2005, Khaliq et al. 2014).

I performed a phylogenetic principal component analysis (pPCA) on the bill measurement data using the “BM” correlation structure and trait covariance matrix in the R package *phytools* (Revell 2009, Revell 2012). A pPCA takes phylogenetic relatedness into account, calculating summary axes that are concordant with a Brownian Motion model of evolution and thus satisfying the assumptions of our phylogenetic comparative analyses (Uyeda et al. 2015). Principal component analyses performed on a dataset comprising linear

measurements will (nearly) always have the first pPC axis capture variance in size among the specimens measured (Pigot et al. 2016, Crouch and Ricklefs 2019).

Song processing and measurements

I obtained vireonid song recordings from the Macaulay Library (<https://www.macaulaylibrary.org/>) and xeno-canto (<https://www.xeno-canto.org/>). I used the recording quality rating systems of the two song libraries to select recordings with high signal-to-noise ratios. When possible, I collected 10 song recordings from across the geographic range of each species. For all species, I selected recordings separated in space by at least 2 km, and in time by at least 1 year to reduce the chance of resampling the same individual. For this study, I focused only on male songs for each species.

I viewed each recording as a waveform and spectrogram (Hamming window, FFT size = 512 samples, 87.5% overlap) using Raven Pro sound analysis software (v1.5; Charif et al. 2010), and annotated all high-quality songs (e.g., clear tracings and no overlap with other sounds on the spectrogram, and clear amplitude pulses on the waveform). I defined a song as a vocalization comprising one or more elements, and elements as a continuous trace on the spectrogram. Elements of a single song were separated by < 0.5 s, and successive songs were always separated by ≥ 0.5 s of silence. I chose 0.5 s because it reflects the minimal length of silent periods that separate elements of separate songs for all vireonids I studied. I used a random number generator to select one annotated song per recording. Selected songs were exported as standalone clips with 0.3 s of silence before and after the song to act as a buffer, filtered with a 600-Hz high-pass filter, and normalized to a peak amplitude of -1 dB.

For each selected song, I visually identified and marked the start and end of each song element by inspecting the waveform and corresponding spectrogram. Previous song analyses have also measured the duration of silences among song elements (Nemeth et al. 2001, Sosa-López and Mennill 2014). but this was not possible for some of our species because they contained only a single element. I divided the song into 2-ms time bins using the “split border” function in Raven and recorded the peak frequency (i.e., the frequency where the greatest power occurs) of each bin within each element. From these raw data, I calculated four discrete song traits that were applicable to all species, regardless of song complexity: (1) song length (s), (2) minimum peak frequency (Hz), (3) maximum peak frequency (Hz), and (4) frequency modulation (Hz per second). Song length was defined as the interval from the onset of the first song element to the offset of the last. Minimum and maximum peak frequency were the 5th and 95th percentiles, respectively, of all peak frequency values from all 2-ms time bins within a song (excluding silent periods between elements). I used the 5th and 95th percentiles, rather than the minimum and maximum values, because they are less likely to be artifacts or outliers that misrepresent the acoustic space used by a given species (Podos et al. 2016, Fahmy and Wilson 2020). Finally, I calculated frequency modulation as the cumulative absolute change in peak frequency between all consecutive 2-ms time bins (excluding silent periods between elements), divided by the cumulative duration of all elements. My measure of frequency modulation is similar to the measure of frequency excursion developed by Podos et al. (2016), except that it does not include changes in frequency that occur between the end of one element and the beginning of the next, since some of our species produced songs with only one element. For this same reason, I did not analyze the duration of the silences among song elements, as done in previous studies (Nemeth and Winkler 2001, Sosa-López and Mennill 2014).

Statistical analyses

I measured phylogenetic signal in the four song traits, followed by the two morphological traits, using Pagel's lambda (λ) and Blomberg's K , as measured with the "phylosig" function in the "phytools" package (v.3.5.3; Revell 2012) in R. Pagel's λ and Blomberg's K measure the magnitude of phylogenetic signal of a continuous trait assumed to be evolving under Brownian motion (Pagel 1999, Blomberg et al. 2003). Pagel's λ transforms the branch lengths of the original phylogeny, such that the observed trait distribution on the tips matches the pattern expected under Brownian motion on the transformed phylogeny (Pagel 1999, Kamilar and Cooper 2013). Values for λ range from 0, where traits are evolving independently of the phylogeny (weak phylogenetic signal), to 1, where trait divergence is comparable to what would be expected under Brownian motion (strong phylogenetic signal). It is also possible for λ to be larger than 1, indicating traits are more similar than expected under a Brownian motion model (Kamilar and Cooper 2013). Blomberg's K calculates a ratio of observed versus expected trait variance in trait distributions within and between clades (Blomberg et al. 2003). Blomberg's K ranges from 0 (the null expectation) to infinity. Weak phylogenetic signal is detected when $K < 1$, indicating that closely related species are less similar to each other than would be expected under Brownian motion, showing greater trait variance within clades (Blomberg et al. 2003). Strong phylogenetic signal is detected when $K = 1$, which indicates that species' traits evolved under Brownian motion, showing greater trait variance among clades (Blomberg et al. 2003, Kamilar and Cooper 2013). When $K > 1$, closely related species are more similar to each other than would be expected by Brownian motion alone (Münkemüller et al. 2012).

I tested the probability of λ and K being significantly different from 0 by running a series of randomization tests under 10,000 simulations and comparing the resulting distribution of

simulated values to the values generated from the MCC Vireonidae tree. I present the respective P value for both λ and K ; P values detect the presence of any significant, non-zero phylogenetic signal ($P < 0.05$), whereas λ and K express the magnitude of the phylogenetic signal. To account for phylogenetic uncertainty in the MCC Vireonidae tree, I calculated λ and K on each of the 100 trees in my distribution with the highest posterior probability to test the robustness of these findings. Preliminary analysis indicated that two species had to be removed from my phylogenetic trees. I removed Steller's Jay (*Cyanocitta stelleri*), an outgroup species used in the original Vireonidae phylogeny, because its vocalizations were complex calls, as opposed to the discrete songs seen in vireonids. Similarly, I removed the Brown-headed Greenlet (*Hylophilus brunneiceps*) from the analysis because its song length was an outlier (i.e., 13.5 sec) compared to the rest of the Vireonidae. Therefore, my final set of phylogenetic trees contained 50 species from the Vireonidae.

I used phylogenetic ANOVAs to test whether vireonids living in the three habitat types differ in the four song traits, using the “phylANOVA” function in the *phytools* package in R (Revell 2012). This function conducts post-hoc pairwise comparisons of means between groups, based on methods described by Garland et al. (1993). To take phylogenetic relatedness into account, I performed the phylogenetic ANOVAs using the MCC Vireonidae tree, and report the global F statistic and P value for each song trait. To account for phylogenetic uncertainty, I ran each habitat phylogenetic ANOVA on the 100 best posterior trees.

I used the *caper* package (Orne et al. 2013) in R to fit multiple, simple phylogenetic generalized least squares models (i.e., pglms) to test for relationships between song structure and morphology. The four song structure traits were included as dependent variables in separate models. Bill shape (pPC2 scores) and body mass (ln-transformed) were included as predictor

variables, and the MCC Vireonidae tree was included to account for shared evolutionary histories among species. I visually inspected the distributions of the residuals of each model using the plot function in R. Any species whose studentized residuals were ≥ 3 were treated as outliers and removed, as recommended by Garland et al. (1992) and Jones and Purvis (1997). Removing these individuals did not change the results with respect to statistical significance of any of our models. To account for phylogenetic uncertainty, I ran all pglms models on the 100 best posterior trees. All statistical analyses were run using R v.3.5.2 (R Development Core Team 2008, R Foundation of Statistical Computing, Vienna, Austria).

Results

Vireonidae phylogenetic tree

My Bayesian analysis of the ND2 alignment for Vireonidae achieved convergence after 150,000,000 generations with ESS values $> 2,000$ for nearly all parameters in the model. Species-level relationships recovered in the MCC Vireonidae tree were largely concordant with those of Slager et al (2014), especially within the genera *Pteruthius*, *Vireolanius*, *Hylophilus*, and *Pachysylvia*. Species-level relationships within *Vireo*, the largest genus, differed slightly from the Slager et al. (2014) ND2 topology, but the posterior probabilities in our MCC Vireonidae tree (smallest value: 0.47 – largest value: 1; Figure 2.S1) were similar to the posterior values on the same nodes in Slager's phylogeny (Figure 1 in Slager et al. 2014). I also successfully recovered the major clades within *Vireo*, as described in Slager et al. (2014).

Phylogenetic signal in song and morphological traits

I analyzed songs from 359 individuals from 51 species (Table 2.S2). Song structure among the 50 vireonids included in my analyses was diverse: song length (mean \pm SD: 1.1 ± 1.0 s; range: 0.16–5.5 s), minimum peak frequency (2603 ± 546 Hz; 1803–5254 Hz), maximum peak frequency (4207 ± 960 Hz; 2518–6718 Hz), and frequency modulation (18544 ± 8827 Hz/s; range: 814–37610 Hz/s; Figure 2.1). Songs among the eight genera have noteworthy differences. *Pteruthius* produce simple songs that either have a long, rapid, monotonous single element delivery, or, short songs composed of two mournful elements (Figure 2.1). *Erpornis* sings a rapid, high-pitched trill that is either ascending or descending (Figure 2.1). *Hylophilus* produce the longest songs in Vireonidae; these species sing repetitive songs comprising rapid or slow whistles and trills. *Tunchiornis* songs are pure, slowly modulated whistles. *Vireolanius* songs are simple in structure; songs range from an emphatic, monosyllabic element that begins with an ascending note, then subtly descends into a prominent whistle, or, songs that are steady repeats of 3-4 elements of melodic quality (Figure 2.1). *Vireo* possess the greatest structural diversity in the family. Their songs range from monotonous trills, to steady repeats of a single element, to short and long songs of highly modulated, buzzy, and whistling elements (Figure 2.1). *Pachysylvia* songs are all short, containing melodic, highly modulated elements, uttered steadily (Figure 2.1). Lastly, *Cyclarhis* produce whistled songs of 4-6 slowly modulated elements uttered steadily (Figure 2.1).

Vireonids showed significant phylogenetic signal in all four song traits. My metrics of λ and K suggest strong and moderate phylogenetic signal, respectively. Song length exhibited the strongest phylogenetic signal, with longer songs being largely conserved within the *Hylophilus* genus ($\lambda = 1.01$ $P < 0.0001$; $K = 0.62$, $P = 0.0056$; Figure 2.2.A). I found weaker, albeit

significant, phylogenetic signal in minimum peak frequency ($\lambda = 0.88$, $P = 0.0001$; $K = 0.58$, $P = 0.0066$; Figure 2.2.B), maximum peak frequency ($\lambda = 0.90$, $P = 0.0002$; $K = 0.45$, $P = 0.0009$; Figure 2.2.C), and frequency modulation ($\lambda = 0.85$, $P = 0.0001$; $K = 0.51$, $P = 0.0004$; Figure 2.2.D). My phylogenetic signal analysis on the 100 best Vireonidae trees, using my four song traits, corroborated the MCC Vireonidae tree results (Table 2.1). In addition to song traits, bill shape and body size also varied among vireonids (see details in “morphology and song traits,” below) and exhibited moderate to strong phylogenetic signal. More specifically, I found significant phylogenetic signal in bill shape ($\lambda = 0.83$, $P < 0.0001$; $K = 0.59$, $P = 0.0004$; Figure 2.3.A) and body mass ($\lambda = 0.94$, $P < 0.0001$, $K = 0.71$, $P = 0.0004$; Figure 2.3.B). Phylogenetic signal analyses on the 100 best Vireonidae trees, using these two morphological traits, corroborated the MCC Vireonidae tree findings (Table 2.1).

Habitat and song traits

I grouped vireonids into three broad habitat types: woodlands ($n = 30$), shrublands (8), and open woodlands (12). There were no significant relationships between habitat type and any of the song variables. Using phylogenetic ANOVAs, I found that vireonids from the different habitat classes did not differ in song length ($F = 5.31$, $P = 0.079$), maximum peak frequency ($F = 0.71$, $P = 0.701$), minimum peak frequency ($F = 1.11$, $P = 0.575$), or frequency modulation ($F = 5.50$, $P = 0.075$). None of the habitat phylogenetic ANOVA models on the 100 best trees yielded significant results, corroborating the MCC Vireonidae tree results.

Morphology and song traits

I measured 161 museum specimens representing 58 species of vireonids, with all but 10 species represented by three specimens. This dataset was pared down to contain the 50 species

considered in my ND2 phylogeny reconstructed for this study, and then used in the pPCA. The analysis produced six pPC axes, of which the first two explained 89.2% of the variance in the data (Table 2.S3). The first axis, pPC1, explained 72.5% of the variance. The six bill variables loaded positively onto pPC1, suggesting that this axis represents the overall size of the specimens. Indeed, pPC1 explained 63% of the variation in ln-transformed body mass (linear regression: $\beta = 0.95$, $\text{Adj } R^2 = 0.63$, $P < 0.0001$; Figure 2.S2). Thus, I used ln-transformed body mass as a proxy for body size in this study and did not analyze pPC1 scores. In general, the larger-bodied species comprised *Cyclarhis* and *Vireolanius*, whereas the smaller-bodied species comprised *Vireo* and *Pachysylvia*.

The second pPC axis accounted for 16.7% of the variance, which is greater than the remaining four pPC axes' contributions combined. The eigenvector of this axis was positively loaded by both length measurements, negatively loaded by both depth measurements, and only weakly loaded by the width measurements (positively for WBB, negatively for WBN; Table 2.S3). Species such as Rufous-browed Peppershrike (*Cyclarhis gujanensis*) had negative pPC2 scores and relatively short and deep bills, whereas species such as Lesser Greenlet (*Pachysylvia decurtata*) had positive scores and relatively long and shallow bills. I therefore used pPC2 scores (hereafter, "bill shape") to represent bill morphology.

Song length was not related to bill shape (PGLS: $\beta = 0.87$, $\text{SE} = 0.91$, $\text{Adj } R^2 = -0.002$, $F_{1,41} = 0.93$, $P = 0.3410$, Figure 2.4.A) or to body size ($\beta = -0.22$, $\text{SE} = 0.51$, $\text{Adj } R^2 = -0.02$, $F_{1,41} = 0.18$, $P = 0.6722$, Figure 2.4.B). All 100 of the alternative trees produced comparable, non-significant results.

Minimum peak frequency and bill shape were positively related; songs of vireonids with shorter, deeper bills had lower minimum peak frequencies, compared with those with longer,

thinner bills ($\beta = 1267.49$, $SE = 464.11$, $Adj R^2 = 0.12$, $F_{1,48} = 7.46$, $P = 0.0088$, Figure 2.1, 2.4.C). There was a significant negative correlation between minimum peak frequency and body mass ($\beta = -697.15$, $SE = 255.53$, $Adj R^2 = 0.12$, $F_{1,47} = 7.44$, $P = 0.0089$, Figure 2.4.D). A total of 97 of the 100 alternative trees yielded significant results for bill shape, and all 100 alternative trees yielded statistically significant results for body mass.

Songs of vireonids with shorter, deeper bills had lower maximum peak frequencies, compared to those with longer, thinner bills ($\beta = 2666.03$, $SE = 778.48$, $Adj R^2 = 0.18$, $F_{1,48} = 11.73$, $P = 0.0012$, Figure 2.1, 2.4.E). There was a significant negative relationship between maximum peak frequency and body mass ($\beta = -1601.65$, $SE = 426.15$, $Adj R^2 = 0.21$, $F_{1,48} = 14.13$, $P = 0.0005$, Fig 2.4.F). All 100 alternative trees yielded significant results for both bill shape and body mass).

In contrast, frequency modulation was not correlated with bill shape ($\beta = 8288.3$, $SE = 7885.4$, $Adj R^2 = 0.002$, $F_{1,48} = 1.11$, $P = 0.2985$, Figure 2.4.G) or body mass ($\beta = -7413.1$, $SE = 4185.0$, $Adj R^2 = 0.04$, $F_{1,48} = 3.14$, $P = 0.0829$, Figure 2.4.H). None of the alternative trees yielded significant results for bill shape, though four trees yielded significant results for body mass.

Discussion

I tested non-mutually exclusive hypotheses of how the temporal and frequency components of Vireonidae songs evolve. I first showed that phylogenetic history predicted song length, minimum peak frequency, maximum peak frequency, and frequency modulation, as well as bill shape and body mass, which can affect song structure. My phylogenetic comparative

approach then explored relationships between habitat and morphology and each of these four song traits.

All four vireonid song traits possessed significant phylogenetic signal. Pagel's λ indicated that song traits evolved very similarly to Brownian motion, whereas K suggested these traits are moderately more divergent between species than expected under Brownian motion. Across all four song traits, sister taxa showed considerable trait similarity, explaining the presence of significant phylogenetic signal (Fig 2). However, the entire phylogeny revealed that small and large song trait values occurred in all 8 genera, indicating distantly related vireonids produce songs of similar structure, which likely diminished the strength of K. The single temporal trait, song length, showed the strongest phylogenetic signal; longer songs were highly conserved in the *Hylophilus* clade, whereas shorter songs dominated the remaining genera (Fig 2A). Taken together, my metrics show that vireonid song structure has moderate and significant phylogenetic signal.

My results are congruent with previous research that found significant, albeit lower, phylogenetic signal strength in passerine song traits. Such patterns were found in the song structure of antbirds (Thamnophilidae; Gómez et al. 2010) and leaf warblers (Phylloscopidae; Mahler and Gil 2009, Tietze et al. 2015). In addition, my finding that a temporal trait had stronger phylogenetic signal than frequency traits was in accordance with earlier bird studies (Price and Lanyon 2002, Tietze et al. 2015). One possible explanation for the moderate phylogenetic signal is that some traits are innate, and others are learned (Beecher and Brenowitz 2005, Mason et al. 2017). Temporal components, such as element length and syntax, are intimately linked to phylogenetic history in several avian families (Päckert et al. 2003, Cardoso and Mato 2007, Tietze et al. 2008). In contrast, frequency components may be more prone to

rapid structural changes through copying mistakes and improvisation (Payne 1981, Price 1998, Olofsson and Servedio 2008). Nonetheless, my study provides compelling evidence that phylogenetic history contributes to song diversification in Vireonidae and other avian families.

Vireonid morphology also showed significant phylogenetic signal. Like the four song traits, Pagel's λ indicated that bill shape and body size largely conform to Brownian motion. Similarly, both morphological traits exhibited significant K values, yet still less than 1, indicating that closely related species are less similar to each other than would be expected under Brownian motion. Blomberg et al.'s (2003) fundamental paper on the K metric concluded that behavioural traits are more labile than morphological traits. However, my vireonid study did not detect this pattern, as the behavioural (i.e., song) traits and morphological (i.e., bill shape and body size) traits exhibited similar K values. *Cyclarhis* and *Vireolanius* comprised species with the shortest, deepest bills, and largest bodies, whereas longer, thinner bills, and smaller bodies were more prevalent in *Vireo* and *Pachysylvia* (Fig 3A,B). Thus, the presence of phylogenetic signal in traits that constrain bird song has important implications in vireonid song evolution.

Additional avian families with significant phylogenetic signal in bill traits and body size include Hummingbirds (Trochilidae; Puga-Caballero et al. 2020), Leaf Warblers (Tietze et al. 2015), and several South American species (Tobias et al. 2010, Barcelo et al. 2012). This trait evolution could extend to other morphological traits not considered here, including wing length, tarsus length, and tail length. Structural similarity between closely related species is the hallmark of evolution by common descent (Gregory 2008), and the resulting speciation allows birds to interact with different niches and prey items, reducing interspecific competition, as noted in Hawaiian Honeycreepers (Fringillidae) and Darwin's Finches (Losos and Ricklefs 2009).

The acoustic adaptation hypothesis predicts that temporal and frequency components of avian songs are dependent on the size and density of sound-reflecting surfaces in the habitat of the singer (Morton 1975, Boncoraglio and Saino 2007). However, variation in the four song traits considered here was not associated with habitat type. Despite the principles of sound propagation providing a strong basis for the acoustic adaptation hypothesis, results from previous studies are mixed (Boncoraglio and Saino 2007). Relationships between habitat and song traits have been found in the Little Greenbul (*Eurillas virens*; Slabbekoorn and Smith 2002), Malagasy Paradise Flycatcher (*Terpsiphone mutata*; Van Dongen and Mulder 2006), and White-crowned Sparrow (*Zonotrichia leucophrys*; Derryberry 2009), but not in the Indigo Bunting (*Passerina cyanea*; Hylton and Godard 2001), some corvid species (Corvidae; Laiolo and Rolando 2003), and several Australian songbirds (Blumstein and Turner 2005). Even when some studies found significant habitat effects on song traits, some of their results deviated from the predicted direction of the acoustic adaptation hypothesis. Mason and Burns (2015) found that habitat explained only three out of 10 Tanager (Thraupidae) songs traits, and, of these, only one (i.e., frequency modulation being higher in non-forested habitats) followed the directional predictions of the acoustic adaptation hypothesis. One explanation for conflicting results is that broad habitat categories do not capture microhabitat use of singing birds (MacArthur 1958). For example, woodland-dwelling songbirds may vocalize from the tops of tree crowns with less tree density, whereas shrubland songbirds may sing within dense thickets. Broader habitat types might also be problematic with habitat generalists. For example, the Rufous-browed Peppershrike breeds in both open (e.g., gardens and savannahs) and closed habitats (e.g., montane forests) (Brewer et al. 2019); I classified this species as an open woodland bird in my study. Tubaro and Segura (1995) compared the song structure of Rufous-browed Peppershrikes in three broad habitat categories

and found that peppershrikes in relatively open habitats produced lower frequency songs, again contradicting the predictions of the acoustic adaptation hypothesis. These conflicting results could be resolved by quantifying and correlating microhabitat use of individual birds (e.g., song perches) with song traits.

I found significant positive correlations between bill shape and some frequency components of vireonid songs. Species with deeper, shorter bills sang songs with significantly lower minimum and maximum peak frequency, compared to vireonids with longer, thinner bills. (Fig 1, 3A, 3B). A positive correlation between bill morphology and avian song traits also occurred in woodcreepers (Furnariidae; Palacios and Tubaro 2000), Darwin's finches (Podos 2001), and true finches (Fringillidae; Giraudeau et al. 2014, Porter and Smith 2019). Birds with larger bills cannot manipulate their gape size with the height necessary for higher frequencies (Podos 2001). Hoese et al. (2000) compared song frequency components in sparrows with temporarily immobilized bills to those with unhindered bills and found that songs produced from immobilized bills suffered frequency constraints. Previous research proposed that selection may drive the diversification of bill shapes and sizes across species for optimal capture and consumption of different food items, and that these changes in bill size may, in turn, affect song traits (Herrel et al. 2009). For example, vireonids with shorter, deeper bills, like the Rufous-browed Peppershrike and Chestnut-sided Shrike-Vireo (*Vireolanius melitophrys*), consume larger, hard food items, including beetles, small frogs, lizards, large (~ 70 mm) caterpillars, and Hawthorne apples (Schaldach 1963, Barlow and James 1975, Brewer et al. 2019), and they sing songs with lower frequencies. In contrast, vireonids with longer, thinner bills, such as the Blue-headed Vireo (*Vireo solitarius*) and the Philadelphia Vireo (*Vireo philadelphicus*), consume small insects (Brewer et al. 2019), and they sing songs with higher frequencies. Contrary to my

predictions, I found no effect of bill shape on frequency modulation and song length. Several tropical vireonids in my study, particularly species in *Hylophilus* and *Tunchiornis*, had longer, thinner bills, yet, their songs were short, low-modulated whistles, suggesting alternative selective pressures are shaping frequency modulation in vireonid songs.

I found significant negative relationships between body size and some frequency traits. Larger-bodied vireonids produced songs with lower minimum and maximum peak frequencies, compared to smaller-bodied vireonids. Similar correlations were found in several birds in Europe (Wallschläger 1980) and the Neotropics (Martin et al. 2011; Derryberry et al. 2018). Bigger-bodied birds have larger syrinxes, which produce lower frequencies. Despite this, I found no relationship between body size and frequency modulation. Some tiny (~ 10 g) species of *Hylophilus* in my study, like Grey-chested Greenlet (*Hylophilus semicinereus*) and Tepui Greenlet (*Vireo sclateri*), produced songs with similar frequency modulation found in the larger-bodied (~ 30 g) vireonids, such as Yellow-browed Shrike-Vireo (*Vireolanius eximius*) and Green Shrike-Vireo (*Vireolanius pulchellus*). As with bill shape, body size, alone, may not explain all frequency components of bird song. My study also found no significant relationship between body size and song length. Relationships between avian body size and temporal song traits are mixed. Body size did not explain temporal features of songs in bush warblers (Cettiidae; Wei et al. 2017) or blue cardinals (Cardinalidae; García and Tubaro 2018), whereas larger thraupids sang slower paced songs than their smaller-bodied counterparts (Mason and Burns, 2015). However, due to vireonid song complexity, I did not take temporal measurements at the individual element level. Therefore, relationships between body size and temporal song traits in the Vireonidae require further investigation.

Additional factors shaping song traits

Sexual selection is arguably the most accepted driver of song structure diversity in birds (Darwin 1896, Searcy and Andersson 1986, Mikula et al. 2020). One mechanism of sexual selection is female choice, where females prefer males with certain song characteristics, which males may learn or inherit (Catchpole 1987). For example, males with larger song repertoires and more complex songs acquire mates faster than males with smaller repertoires, less complex songs (Yasukawa et al. 1980, Buchanan and Catchpole 1997, but see Byers and Kroodsma 2009), and lower song performance (reviewed in Wilson et al. 2014). More recent research, however, suggests sexual selection in bird song evolution is more complicated than just female choice, since female song was shown to be phylogenetically widespread and ancestral in present-day songbirds, and has been frequently lost during passerine evolution, including in vireos and greenlets (Odom et al. 2014). Understanding the degree to which song traits conform to phylogenetic history requires the consideration of other factors and evolutionary processes, in addition to sexual selection.

The songs young passerines hear during their song learning phase can also influence song structure (Beecher and Brenowitz, 2005, Phan et al. 2006). Although this phase marks the acquisition of conspecific song, deviations can occur when learning songbirds make mistakes, such as reproducing heterospecific signals (James 1981). Noteworthy examples among vireonids include White-eyed Vireo (*Vireo griseus*) songs containing Downy Woodpecker (*Picoides pubescens*) calls, and Red-eyed Vireos reproducing Olive-sided Flycatcher (*Contopus cooperi*) songs (Adkisson and Conner 1978, James 1976, James 1981, James 1984). Copying mistakes and improvisation during song learning can lead to additional signal diversity, a process known as cultural drift (Podos et al. 2004). Within the context of my study, habitat and morphology

could each strengthen cultural evolutionary song shifts: different habitats may transmit different frequencies better and thus affect which frequency components are likely to be learned, whereas bill shape variation may make perfect imitation of some songs impossible. Songbirds can also adjust song frequency in response to ambient noise, which reflects song plasticity within individuals rather than fixed population differences (Hu and Cardoso 2010, de Magalhães Tolentino et al. 2018). The behavioural strategies used by singing birds may also influence song structure evolution. For example, birds that regularly communicate over short distances, such as duetting male-female tropical pairs (Langmore 1998, Logue and Hall 2014), may utilize a broader acoustic space because their proximity may minimize signal degradation. In contrast, temperate species that communicate over longer distances, and rarely as duets, may experience greater signal degradation (Fotheringham et al. 1997, Benedict 2008), which could restrict the range of frequencies that could be incorporated into their signals. Similarly, territory size data could provide additional insight into the evolution of song structure. The risk of habitat-induced signal degradation could be higher for species holding large territories, and thus favour songs with low frequencies that degrade less over distance. An interesting possibility, however, is that degradation of long-range signals could benefit receivers by providing reliable information about the signaler's location (Naguib and Wiley 2001). Unfortunately, such natural history is not readily available for many species, including tropical vireonids. This information would lead to the formulation and testing of more rigorous hypotheses on habitat use and the evolution of bird song structure.

Whether birds are migratory or non-migratory is also hypothesized to affect song structure. Songs of migratory species are expected to be under stronger selection because migrants have less time on breeding grounds for mate acquisition and breeding, compared to

resident birds (Catchpole 1982). Consequently, both song repertoire and song complexity are often greater in migratory birds, compared to residents (Read and Weary 1992, Collins et al. 2008). Mountjoy and Leger (2001) explored this relationship in Vireos and found that migratory species sang more complex songs (i.e., repertoire size) than non-migratory species, although migration distance was not related to song complexity. In addition to Vireo, which are predominately temperate migrants, my study included several genera containing year-round tropical residents: *Erpornis*, *Pteruthius*, *Cychlarhis*, *Vireolanius*, *Hylophilus*, *Tunchiornis*, and *Pachysylvia*. Determining whether a significant relationship exists between migratory status and song complexity and other aspects of song structure will require further investigation. I could not test this because my song selection criteria did not discriminate between migratory and non-migratory individuals from temperate vireonid populations.

Conclusions

Taken together, my results support the hypotheses that shared phylogenetic history and morphology shape song structure in Vireonidae, and these two factors are not mutually exclusive. It is plausible that vireonid song structure has significant phylogenetic signal because bill shape and body mass, factors shown to constrain song frequencies, also adhere to the phylogeny. Within the context of evolutionary biology, this rich song diversity could serve as a behavioural mechanism that reduces hybridization and promotes vireonid speciation. Future studies can use playback experiments to assess how receivers respond to divergent songs within the Vireonidae, and whether the structural diversity of song traits functions as a behavioural mechanism for reproductive isolation. If song structure is an effective pre-mating barrier, one would predict stronger responses towards similar sounding stimuli, and weaker responses to

dissimilar songs. The present study advances our understanding of how evolutionary processes shape signals that are critical for reproduction, reproductive isolation, and, ultimately, speciation.

Co-authorship Statement

I am the primary author of Chapter 2; this produced a manuscript which was co-authored by Julissa Roncal, Tyler Imfeld, Sander Boisen, and David Wilson. I collected song recordings from online sound libraries, wrote the entire manuscript, and produced figures, all of which were edited by all coauthors. My supervisor proposed the research topic and wrote R code to extract annotated bird songs from song recordings. Julissa Roncal helped acquire the vireonid sequence data and suggested the appropriate phylogenetic analysis. Tyler Imfeld provided morphological data and, alongside Sander Boisen, wrote the code for statistical analysis. Chapter 2 was peer-reviewed and published: **Mejías, M. A., J. Roncal, T. S. Imfeld, S. Boisen, and D. R. Wilson.** 2020. Relationships of song structure to phylogenetic history, habitat, and morphology in the vireos, greenlets, and allies (Passeriformes: Vireonidae). *Evolution* 74: 2494–2511.

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Tables

Table 2.1. Phylogenetic signal of four song traits and two morphological traits calculated from the Vireonidae MCC tree and the 100 trees with the greatest posterior probability. Minimum and maximum values correspond to the smallest and largest Pagel's λ and Blomberg's K values detected across the 100 trees from the posterior, respectively.

	λ	λ min	λ max	λP min	λP max	K	K min	K max	$K P$ min	$K P$ max
Song Length	1.01	0.89	1.03	< 0.0001	0.0009	0.62	0.49	0.68	0.0027	0.0124
Max Peak Frequency	0.90	0.81	0.96	< 0.0001	0.0007	0.45	0.37	0.51	0.0002	0.0035
Minimum Peak Frequency	0.88	0.85	0.92	< 0.0001	0.0006	0.58	0.43	0.66	0.0004	0.0035
Frequency Modulation	0.85	0.70	0.94	< 0.0001	0.0011	0.51	0.42	0.60	0.0001	0.0011
Bill Shape (pPC2)	0.83	0.80	0.90	<0.0001	<0.0001	0.59	0.46	0.69	0.0001	0.0020
ln (Body Mass)	0.94	0.93	0.97	<0.0001	<0.0001	0.71	0.57	0.83	0.0001	0.0008

Figures

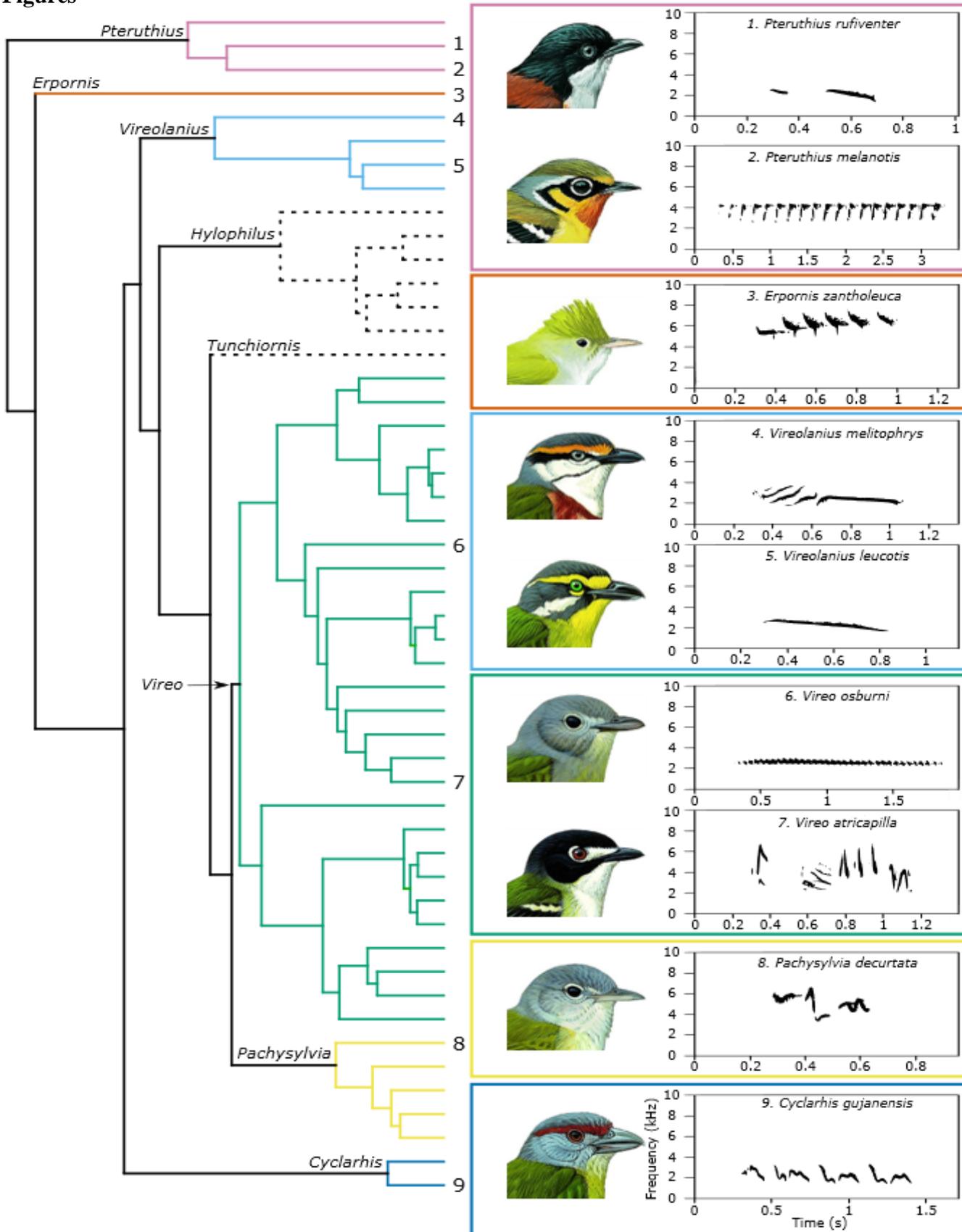
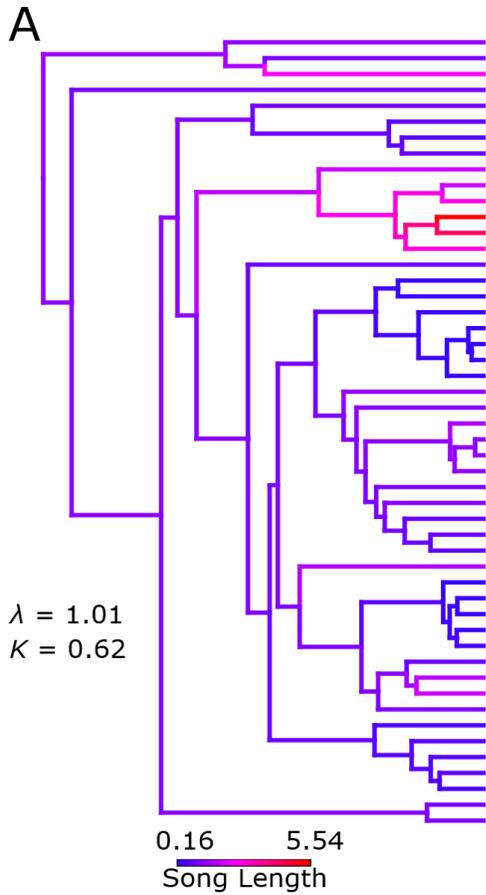
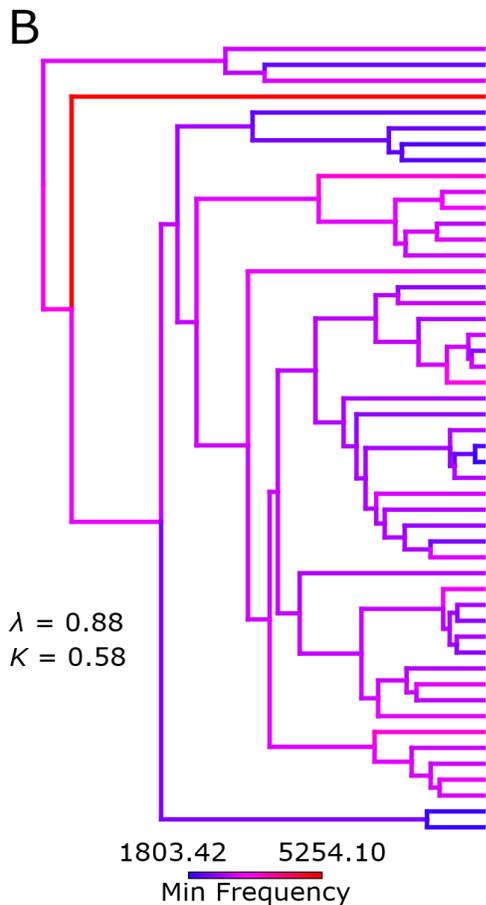
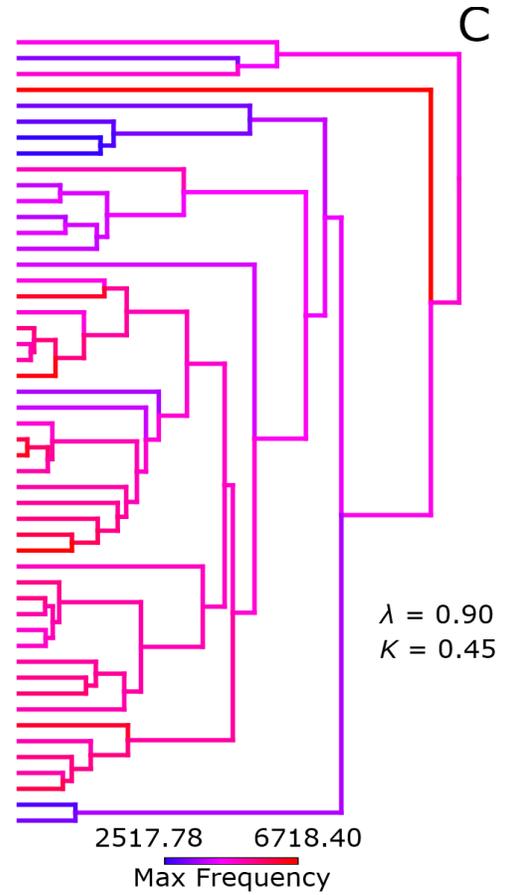


Figure 2.1. Sonograms and illustrations of vireonid species and their relative positions on the MCC Vireonidae tree. The colours of the outlines of spectrograms and illustrations match portions of the tree where species are located. Dashed branches denote clades whose representatives were not depicted with sonograms and illustrations. Species were selected to highlight relationships between bill shape and song structure across the family. Vireonids with shorter, deeper bills produce songs of lower minimum and maximum peak frequency, compared with vireonids with longer, thinner bills. Time on sonogram x-axis is variable to accommodate differences in song lengths. Illustrations reproduced with permission of Lynx Edicions; Brewer, D., R. Orenstein, and A. Bonan. 2019. Vireos (Vireonidae). in J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana (eds.). Handbook of the Birds of the World. Vol. 15. Weavers to New World Warblers. Lynx Edicions, Barcelona.



Pteruthius xanthochlorus
Pteruthius rufiventer
Pteruthius melanotis
Erpornis zantholeuca
Vireolanius melitophrys
Vireolanius pulchellus
Vireolanius leucotis
Vireolanius eximius
Hylophilus poicilotis
Hylophilus pectoralis
Hylophilus olivaceus
Hylophilus semicinereus
Hylophilus flavipes
Hylophilus thoracicus
Tunchiornis ochraceiceps
Vireo vicinior
Vireo huttoni
Vireo flavifrons
Vireo solitarius
Vireo plumbeus
Vireo cassinii
Vireo carmioli
Vireo osburni
Vireo nanus
Vireo pallens
Vireo griseus
Vireo crassirostris
Vireo bairdi
Vireo modestus
Vireo bellii
Vireo latimeri
Vireo brevipennis
Vireo atricapilla
Vireo hypochryseus
Vireo flavoviridis
Vireo olivaceus
Vireo magister
Vireo chivi
Vireo altiloquus
Vireo philadelphicus
Vireo leucophrys
Vireo gilvus
Vireo sclateri
Pachysylvia decurtata
Pachysylvia hypoxantha
Pachysylvia musicapina
Pachysylvia semibrunnea
Pachysylvia aurantifrons
Cyclarhis nigrirostris
Cyclarhis gujanensis



Pteruthius xanthochlorus
Pteruthius rufiventer
Pteruthius melanotis
Erpornis zantholeuca
Vireolanius melitophrys
Vireolanius pulchellus
Vireolanius leucotis
Vireolanius eximius
Hylophilus poicilotis
Hylophilus pectoralis
Hylophilus olivaceus
Hylophilus semicinereus
Hylophilus flavipes
Hylophilus thoracicus
Tunchiornis ochraceiceps
Vireo vicinior
Vireo huttoni
Vireo flavifrons
Vireo solitarius
Vireo plumbeus
Vireo cassinii
Vireo carmioli
Vireo osburni
Vireo nanus
Vireo pallens
Vireo griseus
Vireo crassirostris
Vireo bairdi
Vireo modestus
Vireo bellii
Vireo latimeri
Vireo brevipennis
Vireo atricapilla
Vireo hypochryseus
Vireo flavoviridis
Vireo olivaceus
Vireo magister
Vireo chivi
Vireo altiloquus
Vireo philadelphicus
Vireo leucophrys
Vireo gilvus
Vireo sclateri
Pachysylvia decurtata
Pachysylvia hypoxantha
Pachysylvia musicapina
Pachysylvia semibrunnea
Pachysylvia aurantifrons
Cyclarhis nigrirostris
Cyclarhis gujanensis

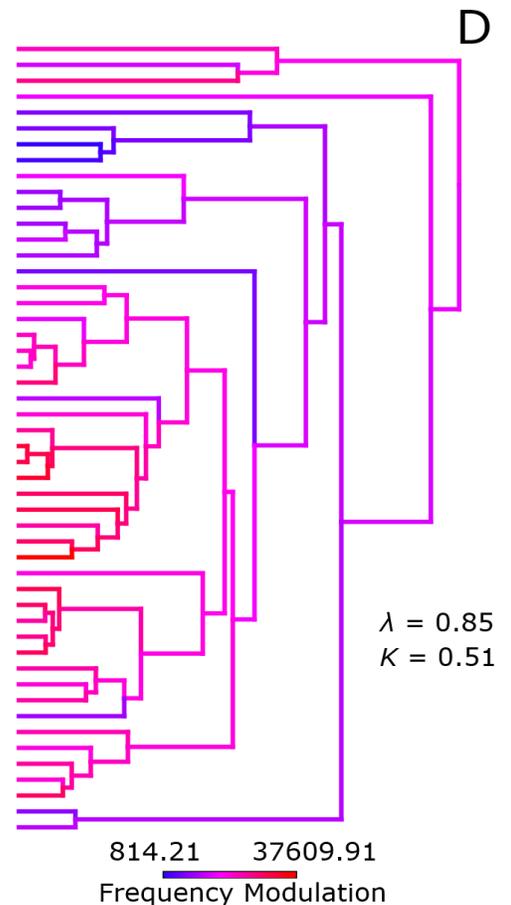


Figure 2.2. Song trait distribution on the MCC Vireonidae tree: (A) song length (s), (B) minimum peak frequency (Hz), (C) maximum peak frequency (Hz), and (D) frequency modulation (Hz/s). Song traits were mapped onto phylogenies using the `plotBranchbyTrait` function in the *phytools* package in R. Colder colours correspond to smaller trait values and warmer colours to larger trait values. Song length showed the strongest song trait conservatism (i.e., phylogenetic signal); longer songs were conserved in the *Hylophilus* clade. The remaining three song traits showed less trait conservatism, with small and large values appearing throughout vireonid genera. The respective magnitude of phylogenetic signal (i.e., Blomberg's K and Pagel's λ) is shown for each song trait.

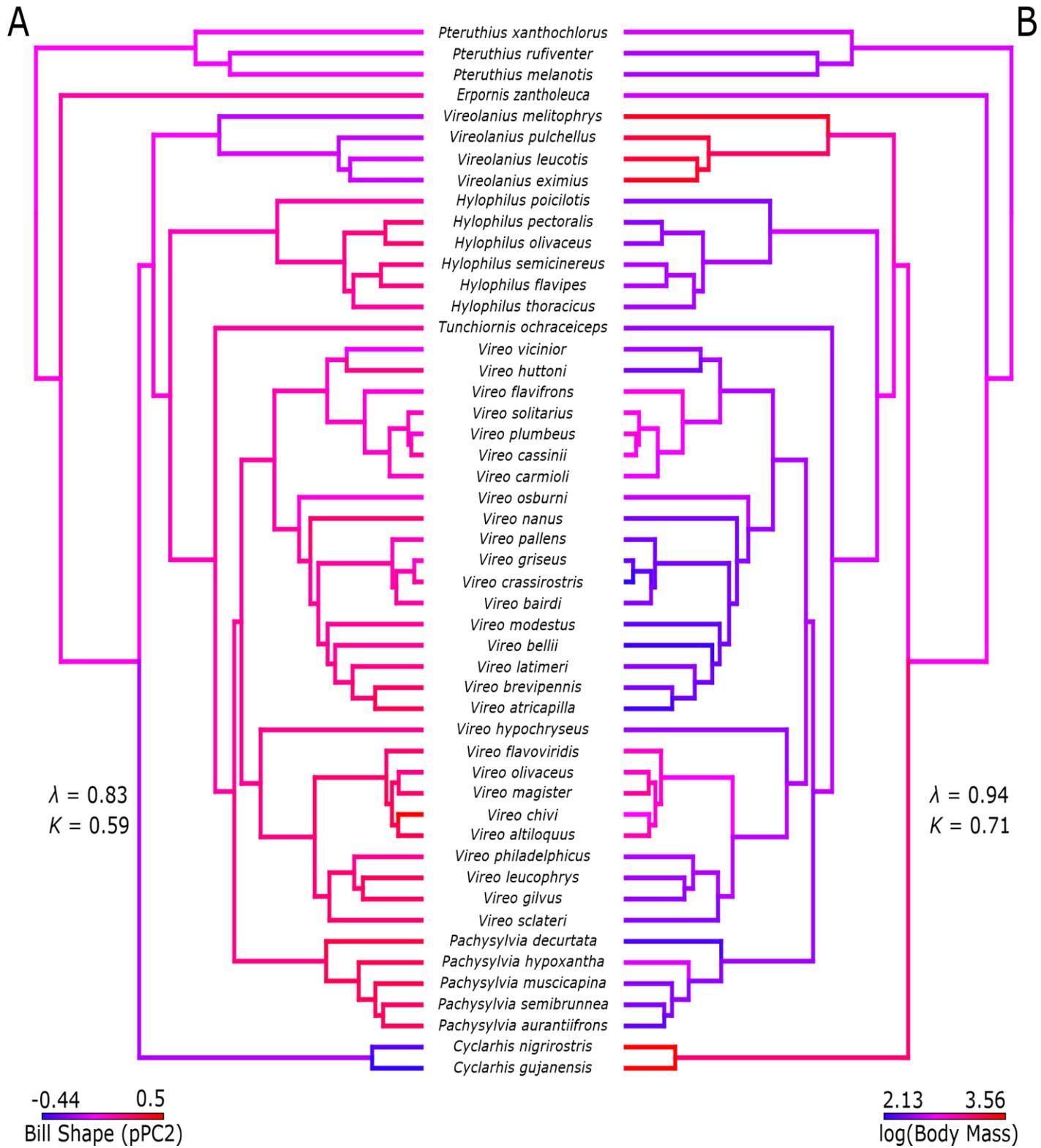
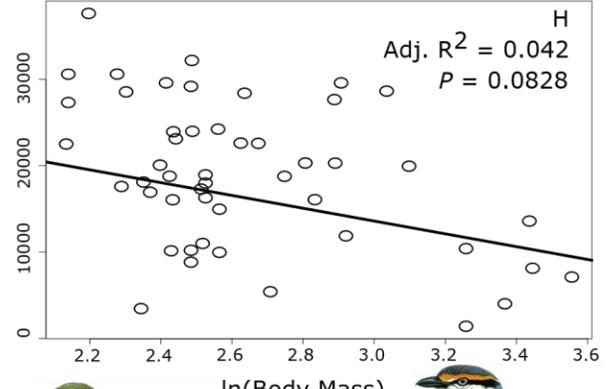
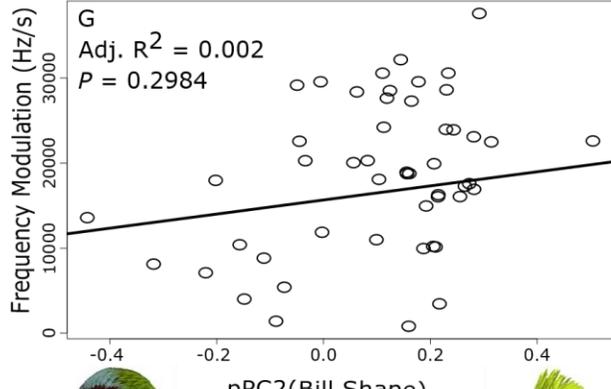
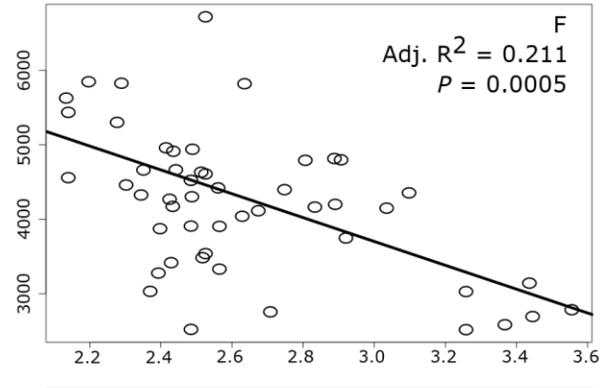
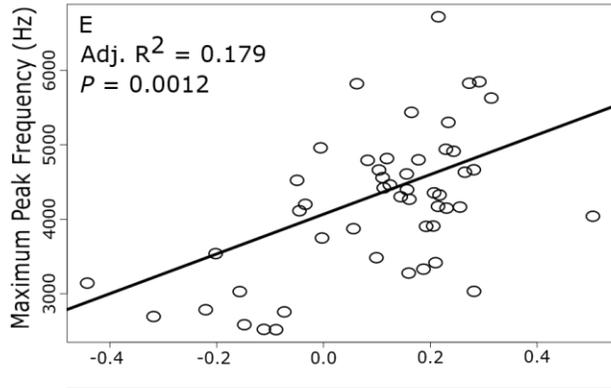
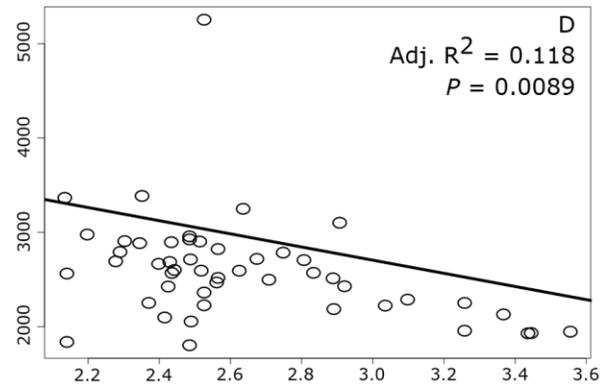
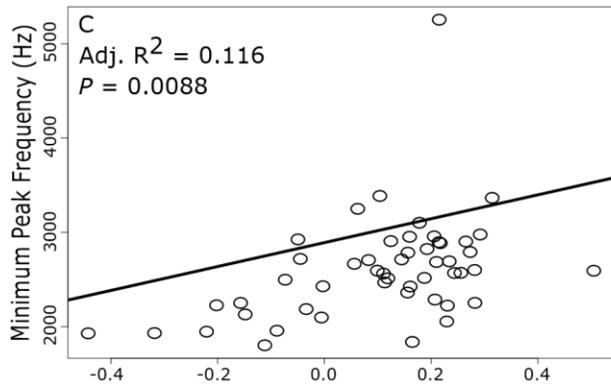
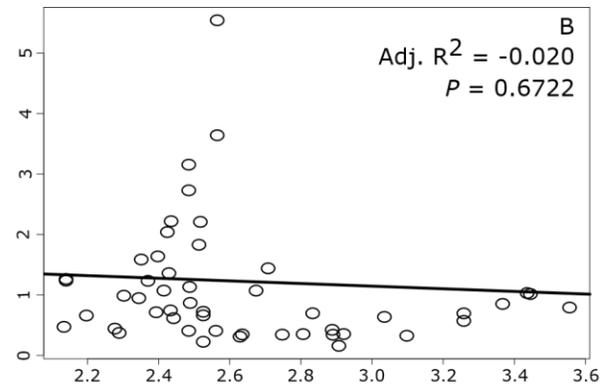
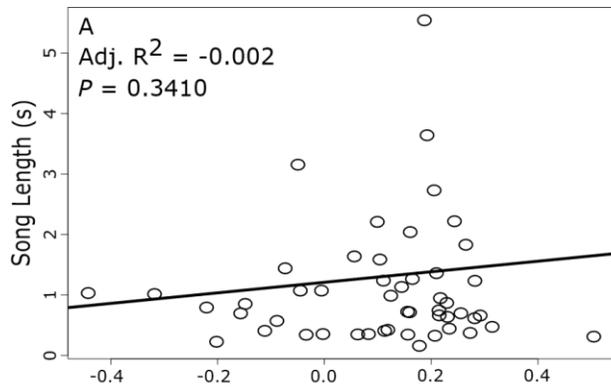


Figure 2.3. Morphology trait distribution on the MCC Vireonidae tree: (A) bill shape (pPC2 scores) and (B) ln(body mass). Both traits were mapped onto phylogenies using the `plotBranchbyTrait` function in the *phytools* package in R. Colder colours correspond to the smaller trait values and warmer colours to larger trait values. Shorter, deeper bills were largely confined to the *Cyclarhis* and *Vireolanius* clades, whereas *Erpornis*, *Hylophilus*, *Tunchiornis*, *Vireo*, and *Pachysylvia* had longer, thinner bills; *Pteruthius* species were intermediate between the two bill extremes. Similarly, *Cyclarhis* and *Vireolanius* contained larger bodies than the remaining six genera. The respective magnitude of phylogenetic signal (i.e., Blomberg's K and Pagel's λ) is shown for both morphological traits.



pPC2(Bill Shape)



ln(Body Mass)



Figure 2.4. Relationships of structure and morphology. Panels in the left column show the relationships between song structure and bill shape (pPC2 scores), whereas those in the right column show the relationships between song structure and body size (ln-body mass). Song structure includes song length (A, B), minimum peak frequency (C, D), maximum peak frequency (E, F), frequency modulation (G, H). Illustrations of Black-billed Peppershrike (*Cyclarhis nigrirostris*) and White-bellied Erpornis (*Erpornis zantholeuca*) depict vireonids with shorter, deeper bills, and longer, thinner bills, respectively. Similarly, Black-eared Shrike-babbler (*Pteruthius melanotis*) and Chestnut-sided Shrike-Vireo (*Vireolanius melitophrys*) depict smaller and larger-bodied vireonids, respectively. Both minimum and maximum frequency showed a significant, positive relationship with vireonid bill shape. In contrast, these same frequency traits showed a significant, negative relationship with body size. Illustrations reproduced with permission of Lynx Edicions; Brewer, D., R. Orenstein, and A. Bonan. 2019. Vireos (Vireonidae). in J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana (eds.). Handbook of the Birds of the World. Vol. 15. Weavers to New World Warblers. Lynx Edicions, Barcelona.

Chapter 3:
Territorial responses of Bermuda White-eyed Vireos (*Vireo griseus subsp. bermudianus*) reflect phylogenetic similarity of the intruder and acoustic similarity of its song*

**This Chapter (Mejías et al. 2021) is the outcome of joint research with J. Roncal and D. Wilson*

Abstract – For signal divergence to drive speciation, receivers should perceive structural differences in divergent signals; similar-structured signals from closer relatives are expected to elicit stronger responses than dissimilar signals from distant relatives. Two mechanisms can affect receiver responses to passerine song: (1) sympatric song familiarity and (2) an innate auditory template used to assess acoustic similarity. I examined the role of acoustic similarity by comparing behavioral responses of male Bermuda White-eyed Vireos (*Vireo griseus bermudianus*) to playback of the songs of allopatric species from across the family Vireonidae. Phylogenetic distance between the focal and stimulus species predicted response strength. Males uttered fewer vocalizations, had fewer speaker flyovers, and remained farther from the speaker during playback of the songs of more distantly related vireos. I then tested whether structural similarity of playback songs, as defined by three phylogenetically conserved song traits, explained these relationships. As predicted, males uttered fewer vocalizations, had fewer speaker flyovers, and remained farther from the speaker in response to more dissimilar songs. Collectively, my results suggest that male Bermuda Vireos perceive and respond to interspecies variation in the phylogenetically conserved song traits of allopatric species of vireos. This suggests that song divergence, and the ability to distinguish divergent songs, reinforces reproductive isolation and competitor exclusion.

Introduction

How birds perceive and respond to conspecific and heterospecific acoustic signals can affect individual fitness. For example, through a sexual selection lens, hybridization may occur if females choose similar sounding heterospecific males as mates (Ficken and Ficken 1967, Willis et al. 2014, Toews et al. 2018). Likewise, interference competition, including males aggressively thwarting mating opportunities of rival males (Grether et al. 2009, Drury et al. 2020), is an important mechanism that prevents hybridization. From an acoustic perspective, reproductive barriers between species can be compromised if males fail to repel similar-sounding heterospecifics from mating with nearby females. Lastly, through a natural selection lens, distinguishing conspecific and heterospecific signals can facilitate ecological competition for important resources, such as food and territories (Losin et al. 2016, Vogt et al. 2017, Gutema et al. 2018, Beltrão et al. 2021). Aside from conspecifics, the risk of hybridization and resource competition from closely related species should be greater than that of more distantly related species because closely related species have more similar signal structures, niches, behaviors, and physiology. In families where the closest phylogenetic relatives tend to live in sympatry (e.g., Parulidae; Simpson et al. 2021), these risks are immediate; in families where the closest phylogenetic relatives tend to live in allopatry (e.g., diverse, tropical montane birds; Freeman 2015), the risks still exist, but are deferred unless secondary contact is made. Therefore, responding more aggressively to closely related species than to distantly related species could further promote and maintain reproductive isolation and resource partitioning.

Bird song facilitates reproductive isolation and speciation by mediating species recognition, mate choice, and interference competition (Borror 1972, Andersson 1994, Slabbekoorn and Smith 2002), allowing receivers to assess the decreasing threat posed by

conspecifics, closely related species, and distantly related species, respectively. Two potential mechanisms underly this assessment. First, being exposed to the songs of conspecifics and sympatric heterospecifics during song learning (Beecher and Brenowitz 2005, Phan et al. 2006) should cause males and females to respond strongly to conspecific signals, and weakly to the songs of heterospecifics that may not pose any threat. This pattern has been found in *Vermivora* warblers (Gill and Murray 1972), *Poecile* chickadees (Hill and Lein 1989), and *Fringilla* chaffinches (Lynch and Baker 1991). The second mechanism is an innate “auditory template” that stores the structural information of an individual’s own song, which can be compared to the songs of another species. Structural similarity between the two signals can determine how the receiver responds (Pinaud and Terleph 2008). In short, songbirds may react strongly to songs that more closely match their own auditory template (Dooling et al. 1992, Brainard and Doupe 2002). Although both learning and acoustic similarity might be important for sympatric species, only acoustic similarity could be relevant for allopatric species where there is no opportunity for juveniles to learn to distinguish their own songs from those of close allopatric relatives. With song familiarity removed, any relationship between the strength of response to a song and phylogenetic distance to the singer would be driven primarily by similarity of acoustic song structure resulting from phylogenetic history (de Kort and ten Cate 2001, Sosa-López et al. 2016). The ability to distinguish close relatives from distant ones based on acoustic similarity could be especially important for families where the most closely related species are allopatric, but where those species then meet in secondary contact.

Playback experiments are a useful tool for investigating the mechanisms underlying avian song recognition. Investigators have used playback experiments to compare receiver responses to the songs of a conspecific and a congeneric, with the general prediction that receivers should

respond more strongly to songs of conspecifics (Greenberg et al. 1993, Linhart and Fuchs 2015, Weir and Price 2019, Darolová et al. 2020). Several songbird species have been found to exhibit this predicted pattern, including Black-capped Chickadees (*Poecile atricapillus*; Kershner and Bollinger 1999), White-eared Ground Sparrows (*Melospiza leucotis*; Sandoval et al. 2013), and Rufous-and-White Wrens (*Thryophilus rufalbus*; Battiston et al. 2015). In other species, however, receivers did not distinguish between conspecific and congeneric songs, e.g., *Hippolais* warblers (Secondi et al. 1999), *Dendroica* (now *Setophaga*) warblers (Pearson and Rohwer 2000), and *Vermivora* warblers (Martin and Martin 2001), possibly because these species exhibit conserved responses to heterospecific songs with phylogenetic signal in their song structures (Mejías et al. 2020). These playback experiments have advanced our understanding of avian responses to acoustic signals, but have involved sympatric species where the two song recognition mechanisms (i.e., song learning and acoustic similarity) were both potentially present. Playback studies with allopatric species remove the potential effect of learning, allowing the independent assessment of acoustic similarity on behavioral responses (Freeman and Montgomery 2017).

Species in the family Vireonidae are ideal for studies of song recognition, with diverse songs learned during development (James 1976a, Mejías et al. 2020). Male responses to song are also conspicuous and easily measured, and are thought to also reflect female responsiveness to those stimuli (Naguib et al. 1999, Illes et al. 2006, Seddon and Tobias 2006). In addition, phylogenetic relationships among the Vireonidae are well-resolved, making broad comparative analyses possible (Slager et al. 2014). Several vireonid song traits, including song duration, minimum peak frequency, maximum peak frequency, and frequency modulation, also exhibit phylogenetic signal, due in part to phylogenetically conserved morphological constraints on song

production (Mejías et al. 2020), and so may provide a basis for discriminating the songs of closely related species from those of more distantly related species. Finally, one vireonid, the Bermuda White-eyed Vireo (*Vireo griseus bermudianus*, known locally as the “*chick-of-the-village*”), is allopatric to all other vireonids, thus removing potential effects of familiarity and learning on receiver responses to other vireonid songs.

My objective was to quantify the behavior of territorial, male Bermuda White-eyed Vireos (hereafter, Bermuda Vireo) responding to songs of diverse species from across the family Vireonidae, including some closely related and others more distantly related. After sequencing the DNA of Bermuda Vireos and adding them to the Vireonidae phylogeny, my first objective was to determine if the strength of receiver responses was correlated with the phylogenetic distance between Bermuda Vireos and the stimulus species. Upon finding that phylogenetic distance predicted behavioral responses, my second objective was to determine if acoustic similarity between the songs of Bermuda Vireos and those of stimulus species explained this relationship.

Methods

Only eight species in the family Vireonidae have been recorded in Bermuda (32°310N, 64°750W; Figure 1), including White-eyed Vireos (*Vireo griseus*), Yellow-throated Vireos (*V. flavifrons*), Blue-headed Vireos (*V. solitarius*), Warbling Vireos (*V. gilvus*), Philadelphia Vireos (*V. philadelphicus*), Yellow-green Vireos (*V. flavoviridis*), Black-whiskered Vireos (*V. altiloquus*), and Red-eyed Vireos (*V. olivaceus*; Amos 1991, Mejías and Mejías 2020). The first seven species are considered rare vagrants, and Red-eyed Vireos are common fall visitors;

migratory vireos are even scarcer in the spring when singing intensifies among temperate passerines. In contrast, Bermuda Vireos, a subspecies of the North American White-eyed Vireo found only in Bermuda, are abundant, year-round residents in the archipelago, and the only vireo that breeds in Bermuda (Mejías and Nol 2020, Mejías 2021). Migrant vireos seldom sing on the archipelago (M. A. Mejías, pers. observ., P. Watson pers. comm.), making Bermuda Vireos largely naive to all songs of heterospecific vireos. As such, I consider Bermuda Vireos allopatric with the North American White-eyed Vireo and all other species in the family Vireonidae.

I conducted fieldwork at 12 sites across Bermuda (Figure 3.1) that were primarily comprised of introduced Brazilian pepper (*Schinus terebinthifolius*), allspice (*Pimenta dioica*), and fiddlewood (*Citharexylum spinosum*). From June to September 2017, I captured Bermuda Vireos along walking trails by luring them into mist-nets using playback of consubspecific songs; these songs were not used in subsequent playback experiments. Each netted bird was fitted with an aluminum Porzana identification band on one leg and either one or two colour bands on the other leg for individual identification. I collected blood samples by puncturing the brachial vein with a 26.5-gauge needle and pressing filter paper onto the wound. Bleeding was stopped by applying a small dab of Clotisol onto the wound and blowing on it gently until it dried. Birds were released at their point of capture within 10 min, and blood samples were labelled and stored in paper envelopes for subsequent DNA sequencing (see details below). I estimated the territory boundaries of colour-banded vireos by opportunistically following them for 1-2 hours during favorable weather from June to September 2017, and marking the GPS coordinates of all perches with a handheld GPS unit (Garmin eTrex® 10, ~3 m accuracy; Garmin International, Inc., Olathe, KS, USA). I found that at least one month of GPS data collection was sufficient to

identify territory boundaries. I mapped territories again before playbacks began in 2018 and, in all cases, found them to be the same as in 2017.

Playback stimuli

To construct playback stimuli, I passively recorded 10 Bermuda Vireo males in their territories during 2017 using a directional shotgun microphone (Sennheiser K6 handheld) and a digital audio recorder (Marantz PMD-661 MKII; WAV format; 44.1 kHz; 16 bits). I continued to record these males until at least two songs with high signal-to-noise ratio and no overlapping sounds were obtained. Some of these 10 males were the same as the 15 used in playback experiments, but I ensured that songs were never played back to the same male from which they were recorded, or to neighbors. To create heterospecific playback stimuli, I obtained song recordings from two online archives (Macaulay Library: <https://www.macaulaylibrary.org/>; Xeno-canto: <https://www.xeno-canto.org/>) for each of the 51 vireonids in the Vireonidae phylogeny (Mejías et al. 2020). When possible, I obtained 10 recordings of each species. I used the recording quality rating systems of the two song libraries to select recordings with high signal-to-noise ratios. To reduce the probability of including multiple recordings from the same individual, I also included recordings of the same species only if they were separated spatially by at least 2 km and temporally by at least one year.

I viewed each recording as a waveform and spectrogram in Raven Pro (Hamming window, FFT size = 512 samples, 87.5% overlap). I annotated all high-quality songs with clear tracings and no overlap with other sounds and clear amplitude pulses on the waveform. I defined a song as an acoustic signal comprising one or more elements, and elements as continuous traces on the spectrogram (Mejías et al. 2020). Elements of a single song were separated by < 0.5 s, and successive songs by ≥ 0.5 s. I chose 0.5 s because it reflected the minimum duration of silent

periods between elements of separate songs for all vireos I studied (Mejías et al. 2020). Female song has been documented in at least four North American vireos (Pitelka and Koestner 1942), whereas information about this behavior in tropical vireos appears undocumented. Although the sex of birds recorded was not known, review of both Macaulay Library and Xeno-canto revealed that all my songs approximate the typical songs for each species.

Consistent with previous descriptions of vireo singing behavior (Borror 1972, Kroodsma 1983), my recordings revealed three distinct singing styles among my study species, including (1) immediate variety, where each new song produced is a different song type, (2) eventual variety, where a single song type is repeated several times before switching to another, and (3) no variety, where a single song type is repeated. Because my goal was to design playback stimuli that matched the natural singing style of each species, I used a random number generator (<https://www.random.org/>) to randomly select two songs (each a different song type) per recording per species for species that sing with immediate or eventual variety, and one song per recording per species for species that sing with no variety. Some species were excluded if (1) I obtained less than two recordings (to reduce pseudoreplication, $N = 2$ species), (2) for a species that sings multiple song types, I had fewer than two recordings containing two or more song types ($N = 10$ species), and (3) song duration was considered an outlier within the family ($N = 1$ species; mean song duration = 13.5 s; Table 3.S1; Mejías et al. 2020). For all retained species, I exported the selected songs as standalone clips with 0.3 s of silence before and after songs, filtered them with a 600-Hz high-pass filter, and normalized them to a peak amplitude of -1 dB. In total, I exported 221 songs from 137 individuals across 38 species (mean number of individuals per species = 3.5 ± 1.9 [SD], range = 1–10; Tables 3.S1 and 3.S2).

I used Audacity software (2.1.3; Audacity Team, 2012; <https://audacityteam.org/>) to create a separate 2-min playback sequence (WAV format, 16-bit amplitude encoding, 44.1 kHz sampling rate) for each of the 137 stimulus males. I standardized the intersong interval of all playback sequences by inserting 5 sec of silence between individual song clips. For species that sing with immediate variety, each playback sequence included two song types from a given individual, presented alternately (i.e., A-B-A-B-A-B-). For species that sing with eventual variety, each sequence included five repetitions of one song type followed by five repetitions of the second song type from a given individual, repeated during the 2-min sequence (i.e., A-A-A-A-A-B-B-B-B-B-A-A-A-A-A-). For species that sing with no variety, each sequence included a single song from a given individual, repeated during the 2-min sequence (i.e., A-A-A-A-A-).

I assigned playback sequences to subjects such that each would be presented songs from species evenly distributed across the Vireonidae phylogeny. To do this, I divided the phylogenetic tree (Mejías et al. 2020) into eight clades and two grades (Figure 3.2). These 10 groups comprised all Vireonidae genera, except the monotypic *Erpornis* because I obtained fewer than two recordings for this species. For each of my 15 subjects, I randomly selected one stimulus species from each of the eight clades and two grades, and then assigned one randomly selected playback sequence, without replacement until all sequences were used, from that stimulus species. Due to the limited number of recordings obtained for some species, some recordings were reused on multiple test subjects. I also assigned one consubspecific playback sequence to each subject. Subjects therefore received two playback sequences from the clade containing Bermuda Vireos (dark green clade in Figure 3.2).

I also created lure sequences with scolding calls of Bermuda Vireos that are often used during agonistic consubspecific interactions (M. A. Mejías, pers. observ.). I elicited scolding calls from

vireos by “pishing.” Scolding bouts were recorded in 2018, prior to playback trials. Using Audacity, I trimmed each recording to a 30-s bout of continuous calls, added 3 s of silence before and after the bout, applied a 1000 Hz high-pass filter, and normalized it to a peak amplitude of 0 dB.

All playback sequences were transferred to a playback device (Apple iPod nano, 7th Generation) for playback in the field. I did not measure the amplitude of the scolding lures or song stimuli during playbacks because I was concerned that the measurement process would disrupt the trial. Rather, because the speaker was calibrated to broadcast a calibration tone (4000 Hz sine wave, normalized to -10 dB) at 80 dB SPL, it automatically broadcast scolding lures (normalized to 0 dB) at 90 dB SPL and songs (normalized to -1 dB) at 89 dB SPL; I confirmed these amplitudes in a series of pilot trials.

Playback experiments

From May to August 2018, I simulated intrusions of consubspecific and heterospecific vireos in the territories of 15 colour-banded male Bermuda Vireos. Intrusions were simulated by broadcasting the songs of the intruding consubspecific or heterospecific for 2 min through a loudspeaker (Monster SuperStar High Definition Bluetooth Speaker; Monster Power, San Francisco, CA, USA) in the subject’s territory. Each subject received 11 treatments in random order, with each treatment presented on a different day to reduce the likelihood of habituation (Sosa-López et al. 2016, Fernández-Gómez et al. 2021). Although 11 trials is more than the number used in some previous playback studies, the within-subjects design provides a powerful test of treatment effects because intermale variability in responsiveness can be accounted for statistically (Akçay et al. 2014). Nevertheless, I acknowledge that subjects may have habituated to the playbacks after repeated trials. I therefore randomized treatment order to prevent any

potential confound between treatment and treatment order and accounted for the potential habituation effects by including trial order in statistical analyses. One treatment included songs of a Bermuda Vireo; the other 10 included songs of heterospecifics from each of the 10 clades composing the Vireonidae (Figure 3.2; see details in 'Playback stimuli,' above). I tested subjects in batches comprising 3–5 individuals from the same general location, and ensured subjects were separated by at least 100 m to reduce the probability that subjects would hear and respond to playback trials conducted in another territory. Within each batch, I randomly selected a maximum of five subjects to test on a given day, repeating this process each day until all males in the batch had received their 11 treatments. All trials were conducted between 08:00 and 13:00 h when there was no precipitation and little to no wind.

Before beginning a trial, I placed the loudspeaker facing upwards on top of a tripod (76 cm above ground) in a natural clearing at the approximate center of the subject's territory. I selected locations where males would be visible for at least 7 m in all directions from the speaker, and with multiple perches at varying distances from the speaker. I chose 7 m because dense vegetation made birds difficult to observe at greater distances. To facilitate distance estimates, I hung coloured trail tape ribbons, 30-cm long, from branches at 1, 3, and 7 m from the speaker in each of the four cardinal directions before trials began; the tape remained in place until all 11 treatments were completed. To calibrate speaker volume, I connected it to the digital playback device, broadcast a calibration tone (4000 Hz sine wave, normalized at -10 dB), and adjusted the volume until the tone measured 80 dB sound pressure level (SPL) measured 1 m from the speaker with a Proster sound level meter ($\pm 1.5\text{dB(A)}$, fast time weighting (125 ms)). I then stood 7 m from the speaker and immediately began the trial.

Trials began by broadcasting an audio lure to attract the subject to the 7-m radius around the speaker, thereby standardizing each male's distance from the speaker before the treatment phase of trials began. The lure was one of 15 recordings (selected at random) of a 30-s bout of continuous Bermuda Vireo scolding calls, flanked with 3-sec of silence before and after the bout. The lure was repeated for 3-min, and the 3-min sequence then played in alternation with 5 min of silence for up to 1 hour. If I observed or heard the subject during the lure playback or a 5-min silence period, I immediately played the lure one final time. Bermuda Vireos move through territories with short flutter hops, which favored my approach of waiting for subjects to approach playback sites after the audio lure ceased. If a subject came within 7-m of the speaker at any time during the 1-h lure phase, I immediately switched to the treatment phase of the trial. Focal males were sometimes accompanied by mates, but I only monitored the behavior of focal males. If focal males did not approach to within 7 m of the speaker before 1 h elapsed, trials were aborted and repeated on another day using a different lure.

When focal males moved within 7 m of the speaker, I began the treatment phase of the trial by broadcasting a pre-selected 2-min song treatment. I recorded the male's behaviour during the 2-min playback and for 1 min after playback. I continued recording even if males left the 7-m radius during either the playback or post-playback periods; recording ceased the moment the test subject left the 7-m radius any time after the 1-min post-playback period. During playback trials, I also quietly dictated the focal male's behavior, including distance from the speaker with each change of perch and the number of flights or flutter-hops over the speaker, into the same microphone used to record focal males.

I subsequently reviewed trial recordings as spectrograms in Raven Pro sound analysis software (1.5; Charif et al. 2010). For each trial, and while the focal male was within 7 m of the

speaker, I counted the number of vocalizations, including songs and scolding calls (Figure 3.3), and number of speaker flyovers. I also noted the distance of closest approach (i.e., perch) to the speaker (1-m resolution) and time spent within 7 m of the speaker. I interpret strong responses as those with many vocalizations and flyovers, and those with close approaches and more time spent within 7 m of the speaker.

Song characteristics

Spectrograms of my playback stimuli revealed that vireonid songs are structurally diverse, thus limiting the number of structural traits common to all species. Following Mejías et al. (2020), I used Raven Pro to measure four song traits applicable to all vireonid songs and that exhibit phylogenetic signal, including song duration, minimum and maximum peak frequency, and frequency modulation. Song duration was defined as the time from the start of the first song element to the end of the last element. To measure frequency traits, I used the “split border” function to split songs into 2-ms time bins, and then automatically determined the peak frequency (i.e., frequency with the greatest energy) of each bin. Minimum and maximum peak frequency (Hz) were the 5th and 95th percentiles, respectively, of the peak frequency values from across all 2-ms time bins across the song (excluding silent periods between elements). Frequency modulation (Hz/s) was the cumulative absolute change in peak frequency across all consecutive 2-ms time bins (excluding silent periods between elements), divided by the cumulative duration of all song elements. For species with two song variants in their playback sequences, I calculated the average between them for each playback sequence. I estimated the four song traits for each species by averaging values from all available playback sequences for that species. To ensure that average song traits were not affected by the number of individuals contributing recordings, I

ran three simple linear regressions where each averaged song trait, per species, was regressed against the number of individuals sampled, per species; all were non-significant (i.e., $P > 0.05$).

Phylogenetic distance between Bermuda Vireos and playback species

To calculate the phylogenetic distance between Bermuda Vireos and each stimulus species, I added the Bermuda Vireo to the existing Vireonidae phylogeny (Slager et al. 2014, Mejías et al. 2020). To do this, I extracted total genomic DNA from 10 Bermuda Vireo blood samples with a QIAGEN DNeasy Blood and Tissue Kit following the blood protocol. The QIAGEN TopTaq master mix kit (Qiagen Inc, Valencia, CA, USA) was then used to amplify the mitochondrial ND2 locus. Amplifications were performed on a 25- μ l solution containing 12.5- μ l TopTaq master mix 2x, 0.4 μ M of each ND2 primer (L5215 and H6313, Brumfield et al. 2007), and ~50 to 116 ng of the template DNA. Thermal cycling conditions were as follows: denaturation at 94°C for 30 s, followed by 40 cycles of 94°C for 30 s, annealing temperature range of 56° to 60°C for 45 s, and 72°C for 1 min. This was followed by a 10-min extension at 72°C. I sent samples to the Centre for Applied Genomics at the Hospital for Sick Children (Canada, <http://www.tcag.ca/>) for Sanger sequencing. The resulting chromatograms were observed, assembled, and edited in Geneious 7.1.8 (<https://www.geneious.com>, Kearse et al. 2012). I aligned the 10 Bermuda Vireo ND2 sequences with the full Vireonidae ND2 alignment from Slager et al. (2014) using MAFFT 7.271 (Katoh and Standley 2013), followed by manual refinement. I conducted a Bayesian inference in BEAST v2.5.2 (Bouckaert et al. 2014), tested for tree convergence in Tracer v1.7 (Rambaut et al. 2018), and generated a maximum clade credibility (MCC) tree in Tree Annotator v.2.5.2 (Bouckaert et al. 2014), all following Mejías et al. (2020). All 10 Bermuda Vireos sampled formed a monophyletic group sister to the North American White-eyed Vireo (*V. griseus*). Bayesian branch support values (posterior

probabilities) ranged from 0.47 to 1 and were concordant with those on the same nodes in Figure 1 of Slager et al. (2014). I pruned the Bayesian MCC tree in R using the *drop.tip* function in the *ape* package (3.5.3; Paradis et al., 2004) to include only the 38 (59% of Vireonidae) vireonid species with playback sequences (Figure 3.2). I used the pruned Bayesian MCC tree to calculate the phylogenetic distances (i.e., patristic distance, substitutions per site; the sum of the lengths of the branches that link two species or subspecies in a tree) between the Bermuda Vireo and the other stimulus species using the *distTips* function in the *adehylo* package (3.5.3; Revell, 2012) in R.

Statistical analyses

All statistical analyses were conducted in R (3.5.2; R Development Core Team, 2008, R Foundation of Statistical Computing, Vienna, Austria). Although principal components analysis can be used to reduce the number of correlated response variables, it is inappropriate for repeated measures data (Budaev 2010), particularly when the number of subjects is < 30 (Jiang and Eskrdge 2000). Therefore, I assessed collinearity among my independent and dependent variables using Spearman correlation tests and considered variables for exclusion if highly correlated (Spearman's $\rho \geq 0.4$). For my dependent variables, time within 7 m of the speaker was strongly correlated with the total number of vocalizations ($N = 165$, $\rho = 0.62$). I chose to exclude time within 7 m of the speaker because it was based on estimated distances and thus prone to error. My remaining response variables (i.e., number of vocalizations and speaker flyovers, and closest approach to speaker) showed low correlation ($N = 165$, all $\rho < 0.4$) and were used as measures of response strength.

For my predictor variables, maximum peak frequency was strongly correlated with frequency modulation (Spearman correlation: $N = 165$, $\rho = 0.85$), so I excluded it from

subsequent analyses. The remaining song traits (i.e., song duration, minimum peak frequency, and frequency modulation) were not correlated ($N = 165$, all $\rho \leq 0.4$). I therefore used these traits that all exhibit phylogenetic signal (Mejías et al. 2020) to estimate the overall acoustic distance between the structure of an average Bermuda Vireo song and the structure of each playback stimulus. To do this, I rescaled each song trait to between 0 and 1, and then treated these scaled traits as the x, y, and z axes of a three-dimensional acoustic space. I then calculated the Euclidean distance between each stimulus song and the mean Bermuda Vireo song in three-dimensional acoustic space (Simpson et al. 2021).

I used linear mixed models and generalized linear mixed models in the lme4 package (Bates et al. 2015) to test my prediction that males respond more strongly to the songs of more closely related species. I regressed each dependent variable (total vocalizations, number of speaker flyovers, and closest approach) against phylogenetic distance, which was included as a fixed effect in three separate models. If relationships were significant (see Results), I tested my second prediction that that these relationships could be explained by the acoustic distance between the Bermuda Vireo's song and stimulus songs. Specifically, I regressed each dependent variable against acoustic distance, which was included as a fixed effect in three separate models. For all six models, subject identity was included as a random factor to account for possible dependencies among repeated trials from the same subject. I also included trial number (1–11) as a covariate with fixed effects to account for any effect of trial order and habituation on responses.

To ensure that my method of attracting focal males using consubspecific calls did not prime subjects to respond weakly to subsequent heterospecific song (i.e., mismatched stimuli) and strongly to subsequent consubspecific song (i.e., matched stimuli), I re-ran my six statistical

models, but excluded the trials corresponding to the consubspecific treatment. The models yielded similar results, and so I present results for the more comprehensive models that include the consubspecific treatment. I present the results for when the consubspecific treatment is excluded in Tables 3.S3 and 3.S4. Finally, I also ran a separate linear mixed effects model to determine if acoustic distance (dependent) was related to singing style (fixed effect), again including subject identity as a random factor. The overall effect of singing style was assessed with the Anova function in the car package (Fox and Weisberg 2019), and pairwise comparisons among singing styles were conducted using Tukey contrasts in the multcomp package (Hothorn et al. 2008). Due to the small sample size ($N = 15$ males), I chose not to include singing style in the models assessing vireo responses to playback because an additional categorical variable would reduce the statistical power needed to detect treatment effects related to my hypotheses.

For my primary statistical models, number of vocalizations and number of flyovers were modeled using generalized linear mixed models with a negative binomial distribution and Poisson distribution, respectively, and a log link. Closest approach was modeled using a linear mixed effects model. Because I tested three different measures of response strength, I controlled experiment wise type I error by applying a Bonferroni correction at the level of the hypothesis (i.e., $\alpha = 0.05/3$). Results pertaining to the hypotheses were therefore considered statistically significant where $P < 0.0167$.

I used the DHARMA package (Hartig 2020) to validate statistical models. Its diagnostic tests, combined with my visual inspection of scaled residual plots, did not reveal any issues with the distribution of residuals, over- or underdispersion, frequency of outliers, or zero-inflation. I also simulated the responses of all six models and found strong agreement between the simulated data and my original data. Finally, using the *car* package, I calculated variance inflation factors

(VIFs) to test for possible collinearity between the two predictor variables in each of the six models predicting vireo responses. VIFs greater than five indicate possible problems associated with collinearity (Zuur et al. 2010); my greatest VIF was 1.15 (Table 3.1, 3.2). Values are provided as means \pm 1 SD.

Results

The 38 species of vireonids used as playback stimuli produced songs with diverse structures (Table 3.S2, Figures 3.4 and 3.5). Average song traits, across the family Vireonidae, were 0.91 ± 0.75 s duration, 2535 ± 471 Hz for minimum peak frequency, and 18129 ± 8798 Hz/s for frequency modulation. Compared to other vireos, songs of Bermuda Vireos were of intermediate duration (mean = 1.01 ± 0.22 s, $N = 10$) and had high frequency modulation (25327 ± 5485 Hz/s, $N = 10$; Table 3.S2, Figures 3.4 and 3.5A, C).

I conducted 165 trials with 15 male Bermuda Vireos. The number of days needed to complete the 11 playback trials varied among males (mean = 22 ± 7.22 d, range = 11–39 d). Typical responses of males to playback included flutter hopping in the foliage while vocalizing within 7 m of the speaker. Overall, focal males produced 2797 vocalizations during 120 of the 165 trials, including 1663 songs during 110 trials and 1134 scolding calls during 29 trials. Focal males flew over the speaker 42 times during 19 trials and approached to an average minimum distance of 4.0 m from the speaker.

The strength of Bermuda Vireo responses increased with decreasing phylogenetic distance to the stimulus species (Figure 3.6, Table 3.1). When responding to songs of more closely related species, Bermuda Vireos produced more vocalizations, flew over the speaker

more often, and approached the speaker more closely (Table 3.1). Excluding consubspecific stimuli trials, the relationship between the number of vocalizations and phylogenetic distance became non-significant, although all other effects remained the same with respect to statistical significance (Table 3.S3). The strength of responses also increased with decreasing acoustic distance between the songs of Bermuda Vireos and the playback stimulus (Figure 3.6, Table 3.2). In response to more similar songs, focal males uttered more vocalizations, flew over the speaker more often, and approached the speaker more closely (Table 3.2). Excluding trials involving consubspecific stimuli, the relationship between closest approach and acoustic distance became non-significant, although all other effects remained the same with respect to statistical significance (Table 3.S4). In all analyses, the strength of responses was negatively related to trial order, with significantly more vocalizations and flyovers, and closer approaches to the speaker, during earlier trials (Tables 3.1, 3.2, 3.S3, 3.S4). Lastly, acoustic distance between the songs of Bermuda Vireos and those of stimulus species differed with singing style (linear mixed effects model, ANOVA: $X^2_2 = 50.7$, $P < 0.0001$). Species singing with immediate variety had significantly greater acoustic distance than those singing with eventual variety (pairwise comparison: $Z = 2.1$, $P = 0.0382$), and species singing with no variety had greater acoustic distance than species singing with either eventual ($Z = 7.0$, $P < 0.0001$) or immediate ($Z = 4.8$, $P < 0.0001$) variety.

Discussion

I show that male Bermuda White-eyed Vireos distinguish among the songs of vireos based on phylogenetic distance. This relationship was expected because some vireonid song traits exhibit phylogenetic signal (Mejías et al. 2020). Using three phylogenetically conserved

song traits, I derived a single measure of acoustic distance and found that it explained the responses of male Bermuda Vireos. Collectively, my results suggest that acoustic similarity, because of phylogenetic relatedness, plays a significant role in how songbirds perceive and respond to song.

Three limitations to my study are worth addressing. First, I found habituation among subjects, with responses to stimuli decreasing during later trials (Dong and Clayton 2009). Although birds are known to habituate after multiple exposures to the same stimuli (Verner and Milligan 1971, Harris and Haskell 2013), finding such strong habituation when the stimulus species changed between trials was unexpected. Focal males may have habituated to the playback apparatus or to lure calls, resulting in weaker responses in later trials. Second, male status (i.e., paired or unpaired and whether they have nests with eggs or young) can affect singing rates (Liu and Kroodsma 2007), and a subsequent study revealed that male Bermuda Vireos that were building nests, incubating eggs, or feeding young sang significantly less than males without nesting duties (Mejías and Wilson, unpubl. data). I did not determine the pairing or breeding status of males in this study so cannot assess their potential effects on responses by focal males. Lastly, I found that the singing style of vireos, a variable that was not part of my hypotheses, was strongly correlated with acoustic distance. Species that sang with eventual variety, like Bermuda Vireos, had songs most similar to those of Bermuda Vireos. I was unable, therefore, to disentangle the correlated effects of acoustic distance and singing style on the responses of male Bermuda Vireos.

My results support the hypothesis that Bermuda Vireos are sensitive to phylogenetically conserved acoustic traits, as also shown in *Troglodytes* wrens (Sosa-López et al. 2016) and *Streptopelia* doves (de Kort and ten Cate 2001). Similarly, James (1976b) found that Warbling

Vireos responded strongly to conspecific songs and weakly to those two vireos with different song structures, i.e., Red-eyed and Yellow-throated vireos. The heightened responses to songs of consubspecifics and closely related heterospecifics may facilitate speciation through reproductive isolation. Hybridization is commonly reported in some songbird genera, like new-world warblers (Graves 1996, Irwin et al. 2009, Toews et al. 2018), but not among vireos. The few reported cases usually involve vagrancy (e.g., Blundell and Kus 2011, McKee et al. 2016). Similarly, Battey and Klicka (2017) reported introgression among vireonids in the Red-eyed Vireo complex, however, these levels were low, and they propose this hybridization reflects historic rather than present-day gene flow. Thus, divergence in vireo songs may be an effective prezygotic reproductive isolation barrier that reduces hybridization.

Heterospecific vireonid competition is well-documented in continental habitats. For example, *V. olivaceus* and *V. philadelphicus* (Rice 1978, Robinson 1981) breed in sympatry in parts of Canada, where their similarities in foraging behavior (Robinson 1981) and song structures (Barlow and Power 1970, Mejías et al. 2020) are thought to drive their ecological competition (Robinson 1981). Bermuda Vireos, however, are exempt from heterospecific vireonid competition because it is the only member of Viroenidae that breeds on the island. Despite its allopatry, my observations of Bermuda Vireos showing stronger responses to relatives with similar song structure and singing style, such as *V. griseus*, *V. crassirostris*, and *V. brevipennis* (Figure 4), is notable because all three species live in semi-open, shrubby habitat, like White-eyed Vireos (Mejías et al. 2020). This further supports the idea that these three species would be viable contenders for ecological resources if they occurred on the island, making these responses beneficial with respect to competitive exclusion.

At least two perceptual mechanisms may be important in avian song recognition, and disentangling the two depends in part on the extent of range overlap among species. In the first mechanism, receiver responses to songs are learned through previous experience with conspecifics and heterospecifics (Gill and Murray 1972, Matyjasiak 2004). However, I ruled out this mechanism in this study by using the songs of allopatric species as stimuli. The second mechanism, more in line with my results, is an inherent ability to adjust responses based on acoustic similarity (Fallow et al. 2011). Specifically, songbirds use an “auditory template,” a neuronal representation of song that guides song development (Soha 2017). Using this template, songbirds compare elements of heterospecific songs to those of their own song and adjust their responses accordingly. Receivers are expected to show stronger vocal and behavioral responses to songs that generally match their own, even songs of unfamiliar species. The responses of male Bermuda Vireos in my study suggest that they use an innate “template” to identify potential rivals based on acoustic similarity.

My results, along with those of Mejías et al. (2020), provide compelling evidence that significant divergence in song structure and song perception is present among species in the family Vireonidae, and that allopatric passerines have an innate ability to respond to heterospecific songs that most resemble their own. This parallel divergence between song structure and song perception likely contributed to speciation in this family. Thus, my results advance our understanding of how the phylogenetic history and song structure of signalers affects allopatric receivers, and how this may ultimately drive speciation.

Co-authorship Statement

I am the primary author of Chapter 3; this produced a manuscript which was coauthored by Julissa Roncal and David Wilson. I conducted the fieldwork (with the help of my parents), quantified data from field recordings, wrote the entire manuscript, and produced figures, all of which were edited by all coauthors. David Wilson and I came up with the research topic; all three authors contributed to the experimental design. Julissa Roncal and I extracted and sequence Bermuda Vireo DNA, which was funded with her research grant (NSERC Discovery Grant # RGPIN-2014-03976). David Wilson helped with statical analysis and provided field equipment needed to record singing behaviour of the Bermuda Vireo, which was funded by his research grant (NSERC Discovery Grant # RGPIN-2015-0376). Chapter 3 was peer-reviewed and published: **Mejías, M. A. and D. R. Wilson.** 2021. Territorial responses of Bermuda White-eyed Vireos (*Vireo griseus* subsp. *bermudianus*) reflect phylogenetic similarity of the intruder and acoustic similarity of its song. *Journal of Field Ornithology* 92: 431–449.

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Tables

Table 3.1. Relationships between the strength of response of 15 male Bermuda Vireos to playbacks and the phylogenetic distance between Bermuda Vireos and the playback stimulus species. Model results for trial order are also presented. Statistically significant *P* values, relative to an adjusted alpha of 0.0167, are in bold. All variance inflation factors (VIFs) were < 5, indicating low collinearity among model predictor variables.

Model	Factor	Coefficient (± SE)	Test stat	<i>P</i>	VIF
Total	Intercept	3.87 ± 0.42	9.3	< 0.0001	
vocalizations (GLMM)	Phylogenetic distance	-0.03 ± 0.01	-2.5	0.012	1.15
	Trial number	-0.14 ± 0.04	-3.1	0.0019	1.15
Flyovers (GLMM)	Intercept	0.05 ± 0.72	0.1	0.94	
	Phylogenetic distance	-0.16 ± 0.02	-6.5	< 0.0001	1.04
	Trial number	-0.23 ± 0.07	-3.5	0.0004	1.04
Closest approach (LMM)	Intercept	1.58 ± 0.48	3.3	0.0014	
	Phylogenetic distance	0.09 ± 0.02	4.8	< 0.0001	1.02
	Trial number	0.20 ± 0.05	4.1	< 0.0001	1.02

N = 165 trials distributed evenly among 15 subjects. Random effects (variance ± SD) for total vocalizations: 0.19 ± 0.44; flyovers: 2.93 ± 1.71; closest approach: 0.44 ± 0.66, residual = 4.07 ± 2.02. Test statistic for generalized linear mixed model (GLMM) was *z*; test statistic for linear mixed model (LMM) was *t*.

Table 3.2. Relationships between the strength of response of 15 male Bermuda Vireos to playbacks and the acoustic distance between Bermuda Vireos and the playback species. Model results for trial order are also presented. Statistically significant *P* values, relative to an adjusted alpha of 0.0167, are in bold. All variance inflation factors (VIFs) were < 5, indicating low collinearity among model predictor variables.

Model	Factor	Coefficient (\pm SE)	Test statistic	<i>P</i>	<i>VIF</i>
Total	Intercept	4.12 \pm 0.43	9.6	< 0.0001	
vocalizations (GLMM)	Acoustic distance	-2.45 \pm 0.78	-3.2	0.0016	1.07
	Trial number	-0.13 \pm 0.04	-3.1	0.0019	1.07
Flyovers (GLMM)	Intercept	0.56 \pm 0.76	0.7	0.47	
	Acoustic distance	-7.95 \pm 1.40	-5.7	< 0.0001	1.04
	Trial number	-0.22 \pm 0.06	-3.7	0.0002	1.04
Closest approach (LMM)	Intercept	1.99 \pm 0.55	3.6	0.0004	
	Acoustic distance	2.71 \pm 1.02	2.7	0.0083	1.02
	Trial number	0.19 \pm 0.05	3.7	0.0003	1.02

N = 165 trials distributed evenly among 15 subjects. Random effects (variance \pm SD) for total vocalizations: 0.21 \pm 0.46; flyovers: 3.10 \pm 1.76; closest approach: 0.45 \pm 0.67, residual = 4.46 \pm 2.11. Test statistic for generalized linear mixed model (GLMM) was *z*; test statistic for linear mixed model (LMM) was *t*.

Figures

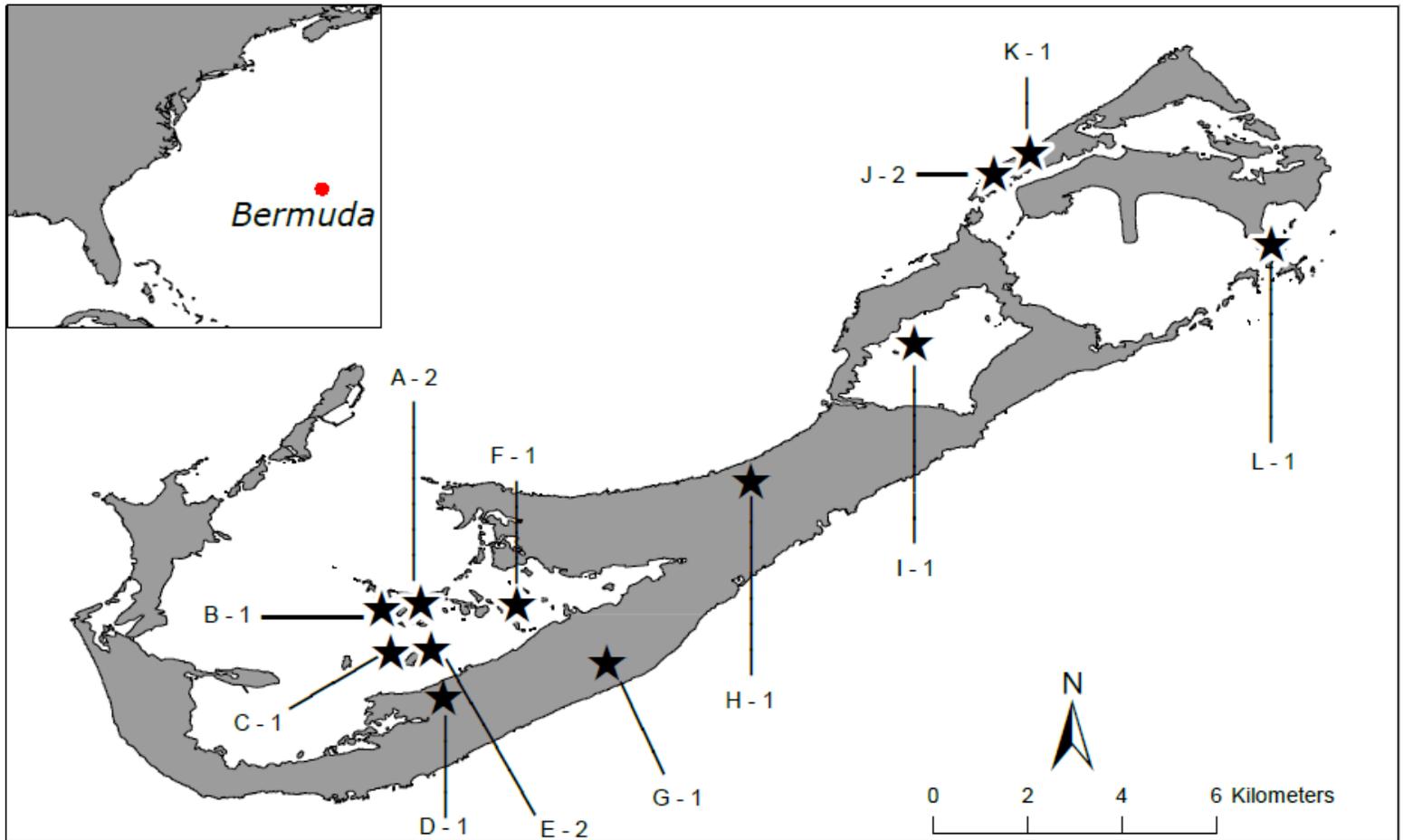


Figure 3.1. Sites across Bermuda where 15 territorial, colour-banded male Bermuda White-eyed Vireos were recorded reacting to playback stimuli. (A) Port's Island, (B) Gamma Island, (C) Burt's Island, (D) Elm Lodge, (E) Darrell's Island, (F) Hinson's Island, (G) Alfred Blackburn Smith Nature Reserve, (H) Oceanview Golf course, (I) Trunk Island, (J) Ferry Reach, (K) Lover's Lake, and (L) Cooper's Island. Numbers represent the number of male vireos recorded, per site.

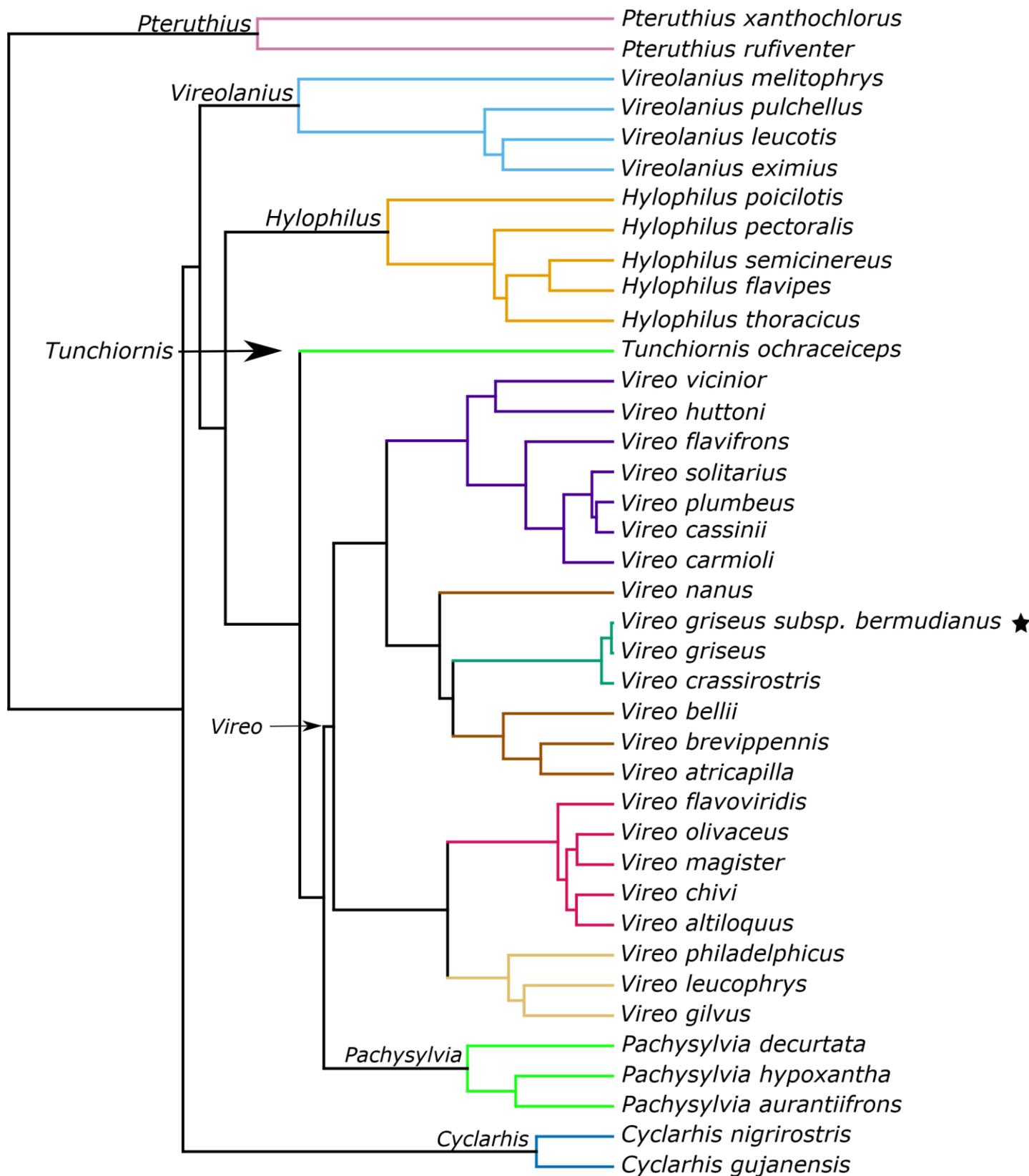


Figure 3.2. Maximum clade credibility (MCC) tree for 38 Vireonidae species and Bermuda White-eyed Vireo subspecies (marked with a star) used as playback stimuli. I performed a Bayesian analysis in BEAST v2.5.2 using ND2 sequence data from Slager et al. (2014) and my 10 Bermuda Vireo ND2 sequences. I partitioned the phylogenetic tree into eight clades and two grades, each represented by a different colour, to facilitate assignment of diverse playback stimuli to test subjects. From top to bottom: (1) dark pink: *Pteruthius* clade, (2) light blue: *Vireolanius* clade, (3) gold: *Hylophilus* clade, (4) lime green: *Tunchiornis* and *Pachysylvia* grade, (5) navy blue: *Vireo* clade 1, (6) dark brown: *Vireo* grade, (7) dark green: *Vireo* clade 2, (8) dark red: *Vireo* clade 3, (9) light brown: *Vireo* clade 4, and (10) dark blue: *Cyclarhis* clade.

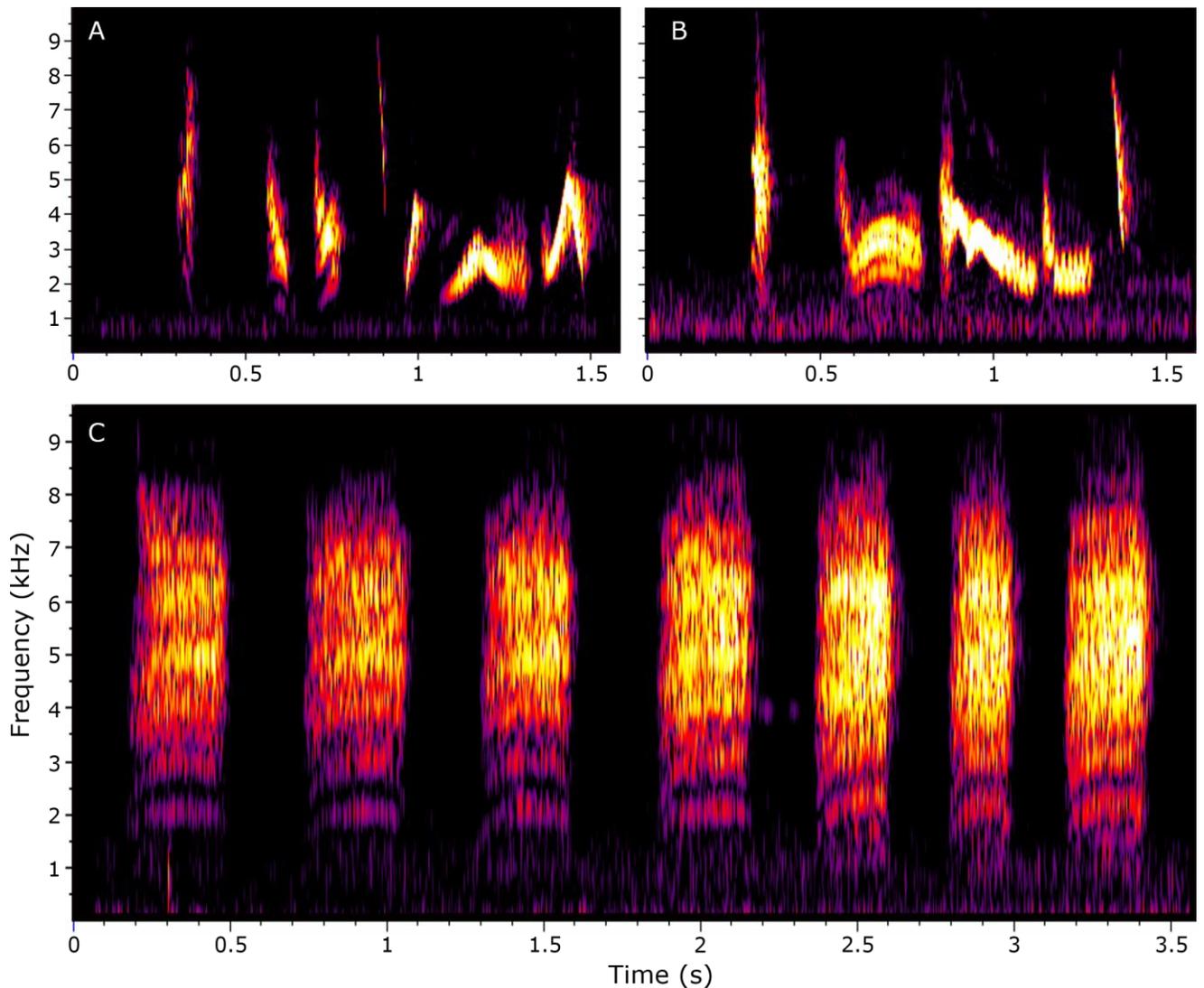
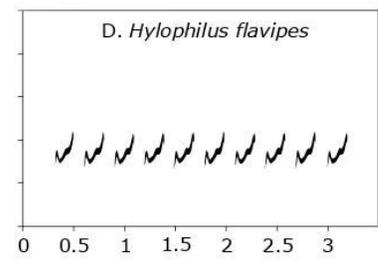
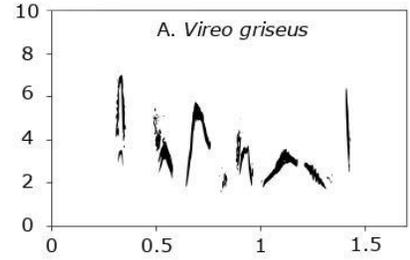
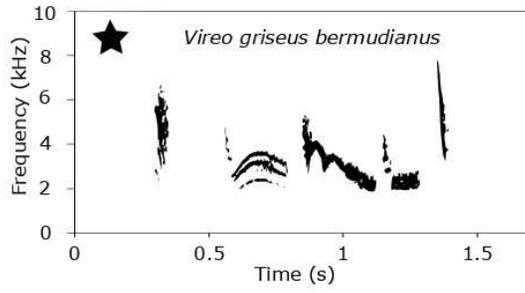
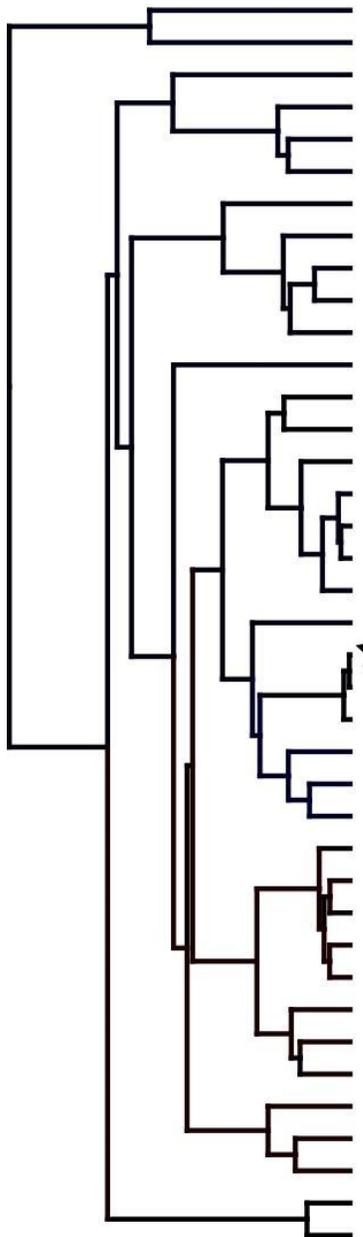
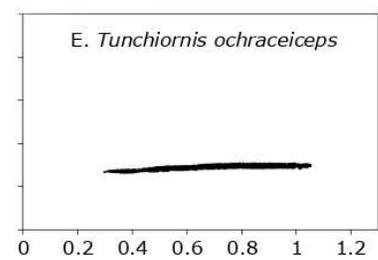
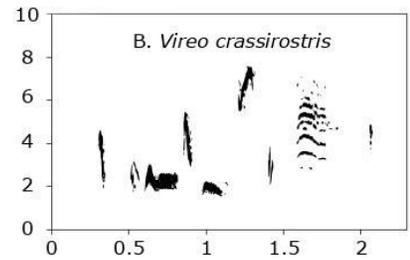


Figure 3.3. Spectrograms depicting two kinds of vocalizations produced by Bermuda White-eyed Vireos during territorial encounters: discrete songs (Bradley 1980; A and B) and scolding calls (C). Discrete song is produced only by males, whereas scolding calls are produced by both sexes. The two discrete songs were recorded from the same male. Note the differences in element structure, representing two discrete song types. Bermuda Vireos sing discrete songs with eventual variety, repeating the same song type several times before switching to another. Each male produces approximately 6–10 discrete song types. Spectrograms were created using a Hamming window, 512-point fast Fourier transform, and 87.5% overlap.



★
A
B
C



★
D
E
F

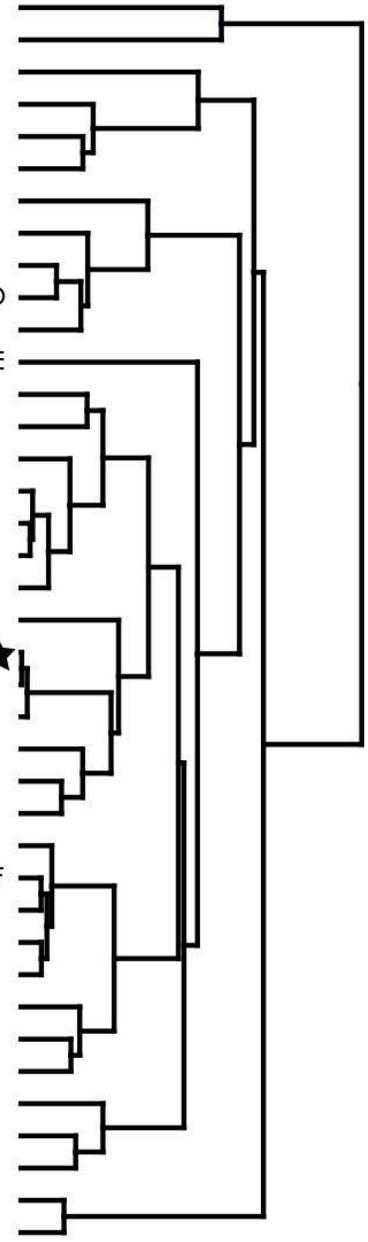
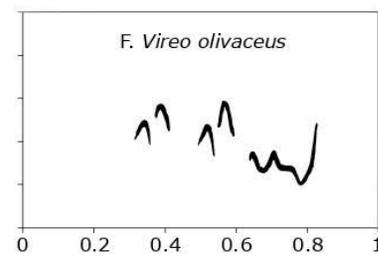
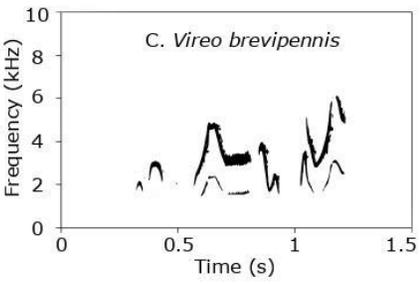


Figure 3.4. Spectrogram of a Bermuda White-eyed Vireo song coupled with spectrograms and illustrations of six other vireonid species and their respective phylogenetic positions. Time on spectrogram x-axes is variable to accommodate differences in song lengths. Species illustrated include three heterospecific vireonids (A, B, and C) whose phylogenetic position and song structure elicited strong vocal and physical responses in Bermuda Vireos (“star”), and examples of vireonids (D, E, and F) that did not. Vireonids on the left are more closely related to the Bermuda Vireo and have similar acoustic structure to this subspecies, whereas vireonids on the right show greater phylogenetic distances and dissimilarity in song structure to the Bermuda Vireo. Illustrations reproduced with permission of Lynx Edicions; Brewer, D., Orenstein, R., & Bonan, A. (2019). Vireos (Vireonidae). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.). Handbook of the Birds of the World. Vol. 15. Weavers to New World Warblers. Barcelona: Lynx Edicions. (<https://www.hbw.com/node/52375>. Accessed 5 November 2019).

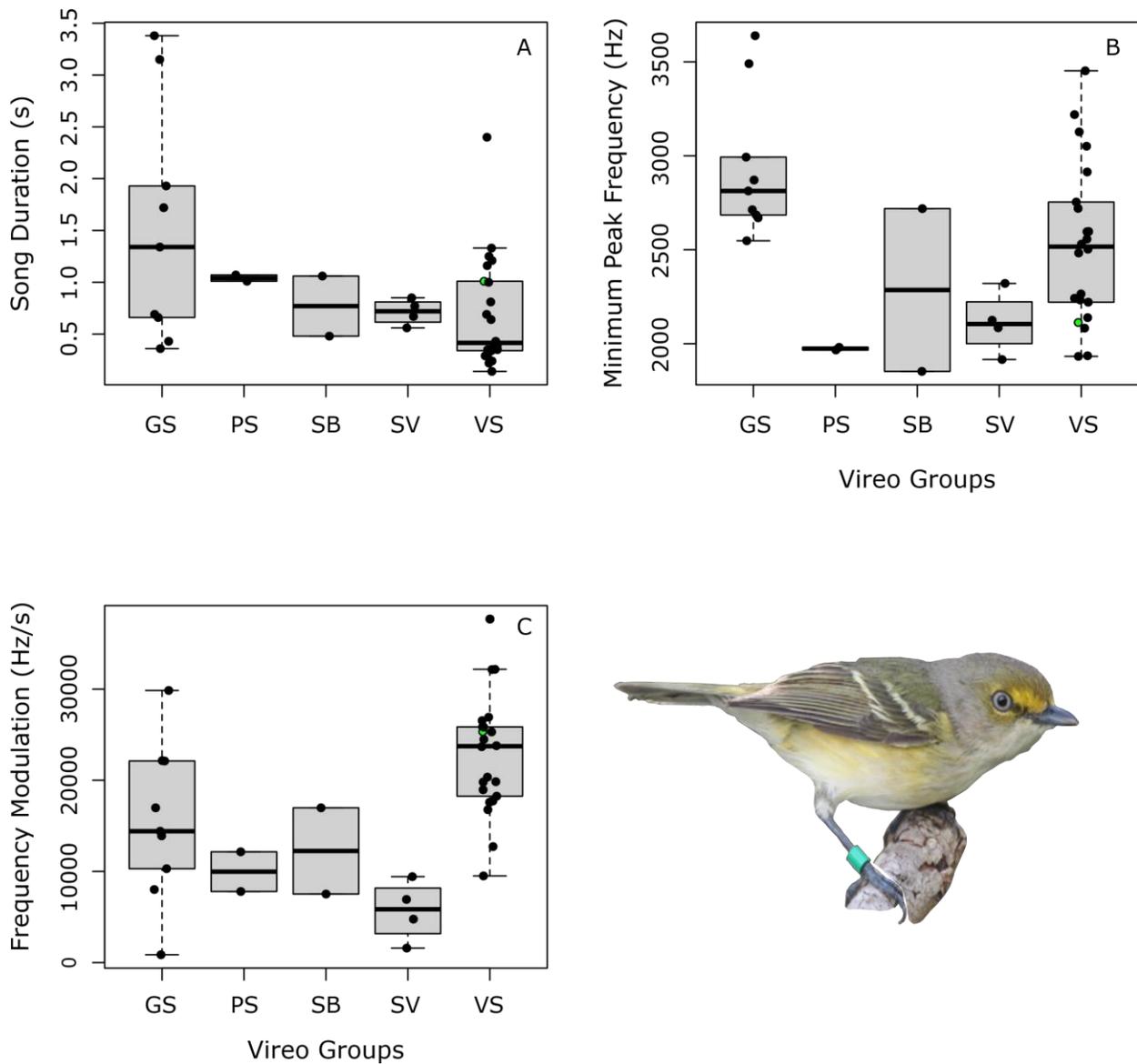


Figure 3.5. Boxplots showing the average song duration (A), minimum peak frequency (B), and frequency modulation (C) of vireonid species' songs across the five following groups: Greenlets (GS), Peppershrikes (PS), Shrike-Babblers (SB), Shrike-Vireos (SV), and Vireos (VS). The Bermuda Vireo is depicted within the Vireo group with a green circle. In general, compared to the other species, Bermuda Vireo songs had an intermediate duration, lower minimum peak frequency, and higher frequency modulation.

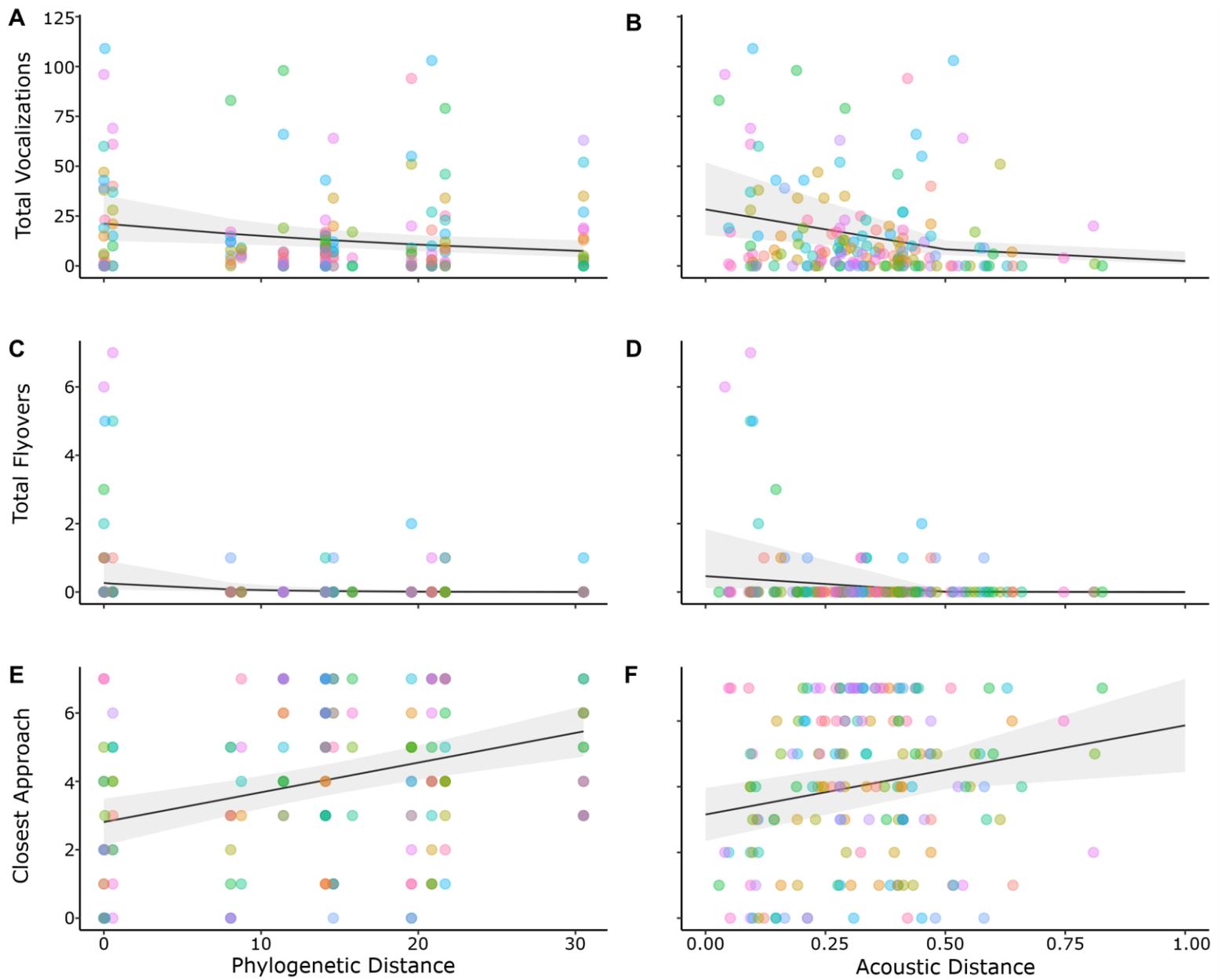


Figure 3.6. Scatter plots depicting relationships of phylogenetic distance and acoustic distance with total vocalizations (A, B), total flyovers (C, D), and closest approach (E, F), respectively. Regression lines and their 95% confidence intervals (clouded, grey outlines) are based on estimated marginal means derived from the statistical models. Different coloured dots correspond to different colour-banded male Bermuda Vireos used as test subjects. A point corresponding to 260 vocalizations is not shown to better illustrate the relationships between

number of vocalizations and patristic distance/acoustic distance (A, B). In general, both vocal displays and number of speaker flyovers significantly decreased with increasing patristic and acoustic distance. A positive relationship was found between closest speaker approach and increasing patristic and acoustic distance.

Chapter 4:
Breeding biology and nesting behaviour of the endemic subspecies of White-
eyed Vireo (*Vireo griseus bermudianus*) on the Bermuda archipelago*

**This Chapter is the outcome of joint research with D. Wilson*

Abstract – Avian, island endemics are prone to extinction and the preservation of remaining taxa requires long term studies on their natural history and threats to survival. Thus, I provide, for the first time, a detailed account of the breeding and nesting threats facing an endemic subspecies of vireonid, the non-migratory Bermuda White-eyed Vireo (*Vireo griseus bermudianus*). From 2016–2021, I located 84 nests, collected breeding data associated with 47 breeding pairs, and conducted observations throughout their nesting cycle. Some breeding pairs remained together for four successive breeding seasons. Compared to continental populations, Bermuda Vireos had a protracted and asynchronous breeding season, from February – September. Both sexes contributed to all nesting stages, which were similar in duration to other vireo species: nest building ($N = 13, 5 \pm 3$ days; mean \pm SD), incubation (11, 14 ± 2 days), nestling care (6, 11 ± 2 days), and fledgling care (5, 41 ± 12 days). Nests, eggs, and nestlings were all vireonine in structure and appearance; nests were found in 14 tree species (2 endemic, 2 native, and 10 introduced). Across six years, 25 of the 42 nests (60%) with eggs produced nestlings, and 10 of the 25 broods (40%) produced fledglings; introduced predators were the primary cause of nest failure (16/27 nests, 59%). The Bermuda White-eyed Vireo is the last endemic, terrestrial bird that breeds on the island and is of local conservation importance. My observations should prove beneficial to other researchers interested in the biology and threats facing breeding vireo species beyond Bermuda, and for creating effective recovery plans necessary for conservation and management.

Introduction

The past four centuries saw approximately 90% of bird extinctions occurring on islands (Johnson and Stattersfield 1990). Humans have directly and indirectly driven the extinctions of endemic, island bird species in three primary ways: (1) introduction of predators and browsing animals, (2) harvesting birds and their eggs, and (3) habitat destruction (Wood et al. 2017). For example, predation from the introduced brown tree snake (*Boiga irregularis*) in Guam and herbivory from introduced domestic rabbits (*Oryctolagus cuniculus domesticus*) in Laysan, respectively, has led to the extinction of the Guam Flycatcher (*Myiagra freycineti*; Savidge 1987) and Laysan Millerbird (*Acrocephalus familiaris familiaris*; Johnson and Stattersfield 1990). The Cuban Macaw (*Ara tricolor*) survived until the mid-19th century, with significant hunting pressures contributing to its eventual extinction (Wiley and Kirwan 2013). Most threatened island bird species live in forests, and tree clearing in lowland areas may have contributed to the extinction of the St. Kitts Bullfinch (*Melopyrrha grandis*; Olson 1984, Johnson and Stattersfield 1990). Compared to continental avifauna, island endemics are likely more prone to extinction due to naivety towards novel threats (Banks and Dickman 2007) and very restricted ranges (Biber 2002). The preservation of the remaining island endemic birds requires thorough studies of natural history and threat assessment.

The Bermuda White-eyed Vireo (*Vireo griseus bermudianus*; hereafter Bermuda Vireo) is a small (9–15 g), subspecies of the White-eyed Vireo that can be found foraging in pairs throughout the woodlands, thickets, and marshes of Bermuda where it is endemic (Bangs and Bradlee 1901, Amos 1991). Males are easily identified by their complex song known onomatopoeically as “*chick-of-the-village*”; the song gives the bird its local nickname and is used for mate attraction and year-round territory defense (Mejías et al. 2020; Mejías 2021,

Mejías and Wilson 2021). No official population estimate is available for the Bermuda Vireo, although historical and present-day observations suggest a large, island-wide population. For example, Jones (1859, p. 71) stated that it was “found in abundance all the year round,” and, more than a century later, Amos (1991) echoed those testaments, noting that the birds were common in gardens, mangroves, and woodlands. Mejías and Nol (2020) attributed the Bermuda Vireo's persistence and ubiquity across the archipelago to its habitat generalist lifestyle and tolerance to woodland fragmentation.

According to the fossil record, avian endemism in recent millennia has been lower in the Bermuda archipelago than in other oceanic islands and has continued to decline over time (Sterrerr et al. 2004). Some birds went extinct during the Pleistocene, when episodic sea-level fluctuations caused significant land reductions of the Bermuda Islands between periods of land expansion during glaciation (Olson and Wingate 2001, Olson and Hearty 2003, Olson 2008). Other endemic birds became extinct because of human activity. Following their introduction to Bermuda around the mid-1500s, hogs (*Sus scrofa*) devastated breeding bird populations (Sterrerr et al. 2004, Olson and Wingate 2006, Olson and Wingate 2012, Olson 2013). The early settlers reduced avian populations directly through unsustainable consumption of birds and their eggs (Lefroy 1877) and indirectly through the introduction of mammalian, avian, and insect predators (Lefroy 1877, Sterrer et al. 2004, Mejías et al. 2017). A night heron (*Nyctanassa carinocatactes*; Olson and Wingate 2006), a towhee (*Pipilo naufragus*; Olson and Wingate 2012), and the Bermuda Flicker (*Colaptes oceanicus*; Olson and Wingate 2013) are on the island's list of endemic extinctions. Centuries of tree felling and exotic plant introductions have nearly replaced Bermuda's native forest (Wingate 1990, Sterrer et al. 2004), removing the

indigenous flora endemic birds evolved in. Of the 14 resident landbird species currently inhabiting the island, the Bermuda Vireo is the only remaining endemic form.

Despite its widespread presence in wooded habitats across the island, its conspicuous vocal displays, and docility, the breeding ecology of the Bermuda Vireo remains unknown. I am not aware of any descriptions of nesting behaviour, and historical observations of nests are scant. Reid (1877, p. 14) states that their “pretty pensile nest,” which hangs 0.9–3.7 m above the ground in mangroves and the previously abundant Bermuda cedar (*Juniperus bermudiana*), contained up to 3 white eggs with brown flecks. Based on a small sample size, Crowell and Rothstein (1981) note that clutch size ranges from 2–3 eggs. Given the frequent fate of island endemics and paucity of data on nests and nesting behaviour of Bermuda Vireos, the objectives of this study were to provide fundamental information on breeding ecology, including descriptions of: (1) pair bond duration, (2) breeding phenology and behaviour, (3) nests, eggs, and nestlings, and (4) breeding success and causes of reproductive failure. This information provides a necessary foundation for conservation and management of the Bermuda Vireo and may provide insight into the breeding ecology of other vireos.

Methods

Study sites

Bermuda is an oceanic archipelago (32°18'N, 64°47'W) formed from fossilized, calcareous shell-sand (Verrill 1902). It is located in the western North Atlantic Ocean, approximately 965 km from the closest point along the east coast of North America (Cape Hatteras). This low-lying yet hilly (0 m – 76 m, mean: 38 m) archipelago is subtropical in climate, with sunshine and light winds dominating April-September, and rain and gales are more

common in the winter months (Amos 1991); temperatures across the year range from 18 – 27.5°C. Present-day wooded habitat is dominated by secondary forests of introduced vegetation, including Brazilian peppertree (*Schinus terebinthifolia*), Australian whistling pine (*Casuarina equisetifolia*), Chinese fan palm (*Livistona chinensis*), allspice (*Pimenta dioica*), and Suriname cherry (*Eugenia uniflora*). Although uncommon, some native trees remain, including Bermuda cedar, Bermuda palmetto (*Sabal bermudana*), Bermuda olivewood (*Elaeodendron lananum*), and southern hackberry (*Celtis laevigata*).

Field methods

I observed breeding Bermuda Vireos across the main island and offshore islets from February to September, 2016–2021, although pair bond data was collected up to November 2021 (Figure 4.1). I collected vireo nesting data as follows: nesting observations in 2016 ($N = 2$ nests); 2020 (2); and 2021 (5) were based on chance encounters, 2017 observations (30) were derived from intentional nest searches (this study), and 2018–2019 observations (45) were collected opportunistically while studying Bermuda Vireos in the context of other research focused on singing behaviour (Mejías et al. 2021).

I conducted nest surveys on days with little to no wind or rain, between 0700–1700 h. I found Bermuda Vireos readily by listening for their song or scolding calls (Mejías et al. 2021), and then followed them along walking trails or through thickets during daylight hours and favourable weather. Vireos carrying material could usually be followed to their nests on account of their songs, calls, and tame nature. To reduce changes in their natural behaviour, I stayed at least 5 m from birds when I followed them. During years of haphazard nest encounters, I also found nests along trails or in the foliage on days with little to no wind or rain.

Regardless of the context of nest discoveries, I obtained detailed nest observation data from some nests by watching them with binoculars for 30–60 min per day, every 1–4 days, from a standard location that was concealed by vegetation and at least 5 m away from the nest, to minimize disturbance at nest. Like many island birds, Bermuda Vireos are usually tolerant of humans, and my presence did not trigger any scolding, which is indicative of agitation; scolding calls are also known as “chatter vocalizations” (Bradley 1980) or “alarm chatter” (Hopp 2022). I transcribed their nest activity in field diaries, and, during some nest watches, opportunistically quantified nest visits with a digital wristwatch to note whenever a vireo added nest material, relieved its mate from incubation duties, or brought food to nestlings, in order to quantify activity budgets during these stages.

Sex was determined by song; only males sing the primary species-typical song or “discrete song” (Bradley 1980). My observations of colour-banded birds revealed that male-female pairs remain together and defend the same territories year-round, although pair bonds can end (i.e. separation between pair members) at any time (Mejías 2021). Paired vireos often travelled together while giving “*fit-fit-fit*” calls and engaged in nesting activity with one another inside their territory. I estimated the duration of pair bonds by counting the number of days that breeding pairs remained together inside a territory over the duration of the study period. I only calculated pair duration exclusively on vireos in which both members were colour-banded; this is likely a conservative estimate because some pairs formed before being banded and others remained together after the study period ended. I considered a pair bond to have ended if one of the colour-banded birds was no longer seen travelling or engaged in nesting behaviour with its previously known mate or was no longer associated with the previous mate’s territory. Unbanded pairs were distinguished from other unbanded pairs in the vicinity because they were either

separated by distances exceeding the size of a typical territory (~0.25 ha), or because neighbouring unbanded pairs engaged simultaneously in breeding activities at different locations. For example, two unbanded pairs could be distinguished reliably if they were simultaneously attending their respective nests, since Bermuda Vireos only produce and attend one nest at a time.

I opportunistically determined clutch size for 21 accessible nests by looking inside nests and counting eggs and/or nestlings, generally whenever the parents were absent. I usually took clutch and nest measurements when nests became inactive, due to fledging, nest abandonment, or egg or nestling failure. Once a nest was confirmed to be inactive, either following nest failure or fledging, I determined nest height using a tape measure (± 1 in; converted to ± 1 m) from the bottom of the nest to the ground. For nests that were too high for height to be measured directly, I estimated height to ± 1 m visually, as I done in Chapter 5. I used visual estimates because vireo nests were generally placed low within the nesting tree (~ 5 m from ground) and the thick, invasive vegetation made instruments, such as clinometers, impractical. For descriptive purposes, I identified, whenever possible, the tree species containing the nest, collected the nests once breeding activity ceased, and then identified lichen, plant, and anthropogenic materials composing the nest. I used a ruler to measure the inner nest depth (± 1 mm), and vernier calipers to measure nest length (i.e., from the nest rim to nest base) and the minimum and maximum external nest diameters at the top of the nest (± 1 mm). Finally, if abandoned eggs were present, or if the parents were away from an active nest on an incubation break, I used vernier calipers to measure the maximum length and width of eggs (± 1 mm).

I confirmed fledging by the presence of juveniles giving begging calls while following their parents in the natal territory. During this stage, I adopted the same protocol that I used when

following adults during nest searches. Every 1–4 days, for 30–60 minutes during daylight hours and favorable weather, I followed adults as they fed their young inside their territories, observing them through binoculars from a distance of at least 5 m. Begging calls were constant and loud and helped me to follow the birds, but their usage gradually declined as the young obtained independence over weeks. I considered fledgling care to have ended when young were capturing their own food in natal territories, and were no longer seen being fed by either parent.

Breeding phenology

I defined and estimated the duration of the following breeding stages: (1) nest building, (2) incubation, (3) nestling care, and (4) fledgling care. Nest building is the period when the vireos are adding materials to the nest. For some nests (17), I was confident that I found the nest within the first day of the onset of its construction, as evident by the first few bits of nest material woven onto a branch, and I used data for these nests to estimate the duration of the nest building period. Incubation is the period when parents tended to a clutch. Because I did not approach every nest and inspect its contents, I inferred incubation whenever a parent vireo was seen sitting in the nest throughout the majority of a nest watch ($\geq 70\%$ of nest watch). Female songbirds, including vireos, usually lay one egg per day, and incubation typically begins once the clutch is complete (Lapergola et al. 2012). If I was not confident about the date of clutch completion, determined by confirming maximum number of eggs or nestlings during consecutive, opportunistic viewings of unattended nests, I still inferred incubation behaviour but did not include the nest in the estimate of the duration of the incubation period. Nestling care is when parents feed chicks inside the nest, and fledgling care is when parents feed the young after they have left the nest. I inferred nestling care when I observed parents bringing food to the nest or when the parents perched on the nest rim and looked inside the nest cup. I inferred fledgling care

when either parent was seen feeding young amongst the foliage. Because I did not visit each nest daily, I estimated the transitions between stages as the midpoint between the last day observed in the previous stage and the first day observed in the subsequent stage. My observations of parental behaviour always revealed sequential progression through the nesting stages, suggesting that I identified stages correctly. For example, I never inferred that a nest was at the incubation stage after inferring that it had progressed to the nestling stage; sample sizes vary among breeding stages because some nests (38) were discovered after nest construction and others failed before fledging. I report the percentage of nests with at least one egg that produced hatchlings (i.e., hatching success), and the percentage of nests with at least one egg that produced fledglings (i.e., breeding success).

I identified the cause of nest failure whenever possible. The black rat (*Rattus rattus*), Great Kiskadee, and Argentine ant (*Linepithema humile*) are introduced pest species to the archipelago. They are known predators of Bermuda Vireo eggs and nestlings (Mejías 2021, Chapter 5) and were abundant across all study sites. Ant predation was readily identifiable by the tendency of swarms to cover nests and slowly devour eggs or nestlings. Predation from kiskadee and rats, however, could not be confirmed because I did not have a trail camera, thus, the disappearance of nest contents were attributed to unknown predators. Lastly, some nests were found to crumble at various nesting stages. This was characterized by the unravelling of the nest rim from forked branches, outer wall material sloughing off, or the nest splitting in half. Nest collapse was a gradual process that usually occurred over multiple nest watches, and sometimes resulted in the eggs or nestlings falling out.

Results

Study population

Across the entire study period, I documented the breeding behaviour of 81 individuals, comprising 47 breeding pairs. Just over half ($N = 43$) of the vireos were colour-banded (Figure 4.2) and the other vireos (38) were unbanded. Among my banded birds, 26 were male and 17 were female; together, these formed 18 pairs (one female was involved in more than 1 pair) in which both partners were banded. My sample also included 12 breeding pairs in which both members were unbanded. Unbanded pairs could not be used to infer pair duration, but they provided data on breeding behaviour, nesting success, and nest predation (see “*Breeding phenology and behaviour, and descriptions of nests and their contents*” below).

Pair duration and behaviour

Pair duration varied substantially among 18 colour-banded pairs, with some pairs seen together for as little as 1 day while others were seen together for up to 1360 days (Table 4.1). Among these 18 nesting pairs, I confirmed that 7 made multiple breeding attempts, 1 of which bred across multiple breeding seasons (Male: BBP/; Female: BWG/, 24 May 2017 – 11 February 2021; Table 4.1). Based on a subset of 2019 colour-banded pairs, the number of nest attempts within a single season ranged from 1–4 (3 ± 1 nest attempt, $N = 6$). Following the end of pair bonds, newly unpaired males typically remained inside their year-round territories and increased their singing rate, whereas the newly unpaired females visited the territories of several neighbouring males. I commonly observed pair bonds ending after one or more nest failures. In one case, a pair bond ended after the disappearance of a colour-banded male in December 2019; the female remained in the same territory and was joined by a new, unbanded male. However, in

May 2020, this same female was building a nest with a different neighbouring male who was also colour-banded, apparently having divorced the unbanded male.

Breeding phenology, behaviour, and descriptions of nests and their contents

I found 84 nests in the study and obtained data on phenology for 60 (71%) of these. Information on the number of nests reaching each breeding stage, and the fate of the nests, is summarized in Table 4.2. The nesting season of Bermuda Vireos was long and asynchronous (Figure 4.3).

I observed nest building from 28 February – 24 June, but most pairs built nests in April (Figure 4.3A; Table 4.3). I documented nest building behaviour for 22 pairs and 46 nests. At the start of nest building, males often secured the first piece of nest material on a horizontal, forked branch. Subsequent building activity involved pairs commonly going on collecting trips together within the vicinity of the nest-site, and then returned to the building site together with material. During construction, nests would change from being a clump of plant bits or polyfill stuffing on a forked branch, to a shallow sling of plant and litter fibers, and finally a thick, basket-like structure (Figure 4.4), which hung from the end of forked twigs and supported adults, eggs, and nestlings (Figures 4.5, 4.6). The outer nest wall included strips of plant bark, mosses, lichen, and human refuse. Recognizable nest components included lichen (*Ramalina denticulata*) and bark and leaves from Bermuda palmetto, allspice, and cow cane (*Arundo donax*); polyfill stuffing was the most common kind of human refuse and was found in almost all nests. Adults lined all nests with reddish-brown straw fibers collected from old leaf bases of the Bermuda palmetto and Chinese fan palm. I confirmed 14 nest tree species ($N = 78$ nests), including endemic/native (11, 14%) and introduced (67, 86%) species. Nest measurements are as follows: nest height (mean \pm SD = 3 ± 1 m, range 1 – 7 m, $N = 63$ nests); nest length (71 ± 12 mm, 49 – 116 mm, 34); nest

depth (46 ± 6 mm, 32 – 64 mm, 34); widest outside nest diameter (76 ± 8 mm; 60 – 91 mm, 34); narrowest outside nest diameter (68 ± 8 mm, 53 – 85 mm, 34).

Based on a subset of 25 bouts of nest-building (from 15 different nests), I recorded 99 nest visits by nest-building vireos. On average, building pairs returned from collecting trips after 11 ± 8 min (1–31 min). Once the nest structure was approximately 75% complete, males stopped contributing to nest construction and instead shadowed the female on her collecting trips, flicking their wings in front of the female while she finished the nest. A hiatus usually occurred between nest completion and the onset of egg laying (4 ± 3 days; 1–12 days); the hiatus was not included in the nest construction or incubation duration calculations.

I observed vireos in nests from 31 March – 5 July, with incubation peaking in May and June (Figure 4.3B; Table 4.3). During this stage, I observed 25 pairs and 44 nests. Whilst inside the nest, vireos sat motionless, with only the head, bill, and tail visible above the nest rim (Fig. 4.5). Rarely, males sang while sitting inside the nest cup. More specifically, incubating males sang discrete songs with noticeably longer inter-song pauses. Soon after, the female returned to the nest and relieved the male, which then resumed steady discrete song bouts away from the nest. Based on a subset of 51 bouts of incubation (from 16 different nests), the average duration of an incubation bout was 30 ± 14 min (5–60 min). I observed 24 changeovers, when the incubating bird exited, and its mate entered the nest. Changeovers ranged from 5–53 min (22 ± 12 min). Eggs were pearly white with reddish-brown blotches concentrated on the blunt end (Figure 4.5). Clutch size varied among nesting pairs (3 ± 1 egg, 1 – 4 eggs, 21, Figure 4.7). Egg measurements were as follows: egg length (19 ± 1 mm, 17 – 20 mm, 19), and egg width (14 ± 1 mm, 13 – 16 mm, 19).

I observed nestling care from 21 April – 16 July, with nestling care peaking in May (Figure 4.3C; Table 4.3). Observations from a single brood of 3 nestlings in 2017 revealed that nestlings were altricial at hatching, with rapid growth, feathering, and eye-opening occurring over 9 days (Figure 4.6). I monitored 16 pairs of vireos and 20 nests with nestlings. During this period, both sexes carried food in their bills, including insects, caterpillars, spiders, and *Anolis* lizards. After delivering food to the nest, parents removed white nestling fecal sacs from the nest and consumed them at the nest or dropped them several meters away. During the first 3–4 days of nestling care, at least one parent remained at the nest, either perched on the nest rim looking inside, or brooding the naked young; the mate was usually away collecting food. As nestlings aged, both parents went independently on foraging trips. Among a subset of 19 nestling feeding bouts, I recorded the duration of 113 individual nestling feedings trips from 7 different nests (14 ± 12 min; 3–43 min).

I observed fledglings being reared from 30 April – 11 August; fledgling care peaked in May and June (Figure 4.3D; Table 4.3). I followed 5 pairs of vireos caring for 5 broods of fledglings. Throughout this stage, adult vireos gleaned food from the canopy foliage and branches while constantly being followed by their young, which trailed close behind while emitting begging calls and vibrating their wings. Despite being paired, the two parents ceased traveling together during fledgling feeding. Rather, observations from all colour-banded pairs revealed that the parents split the brood during this period. Fathers, which use conspicuous, discrete song to guide fledglings, reared young inside their own territory, whereas mothers, who do not sing, attended the young either in or outside the natal territory; if the latter, this was usually done briefly inside neighbouring territories. Parental aggression towards perceived threats, such as human observers, intensified after fledging. Females seemed to be more

responsive to my presence and gave bouts of scolding calls when I was present anywhere in the natal territory. In contrast, males usually did not react defensively to my presence. In response to their parents' scolding calls, fledglings ceased begging calls and remained motionless in the foliage. I considered the fledgling care to be over when the fledglings no longer emitted begging calls; after that point, they remained in their natal territories but no longer followed or were fed by their parents, and they sometimes helped defend natal territories with scolding calls. Banding data from another study (Mejías and Watson, unpubl. data) revealed that fledglings do eventually disperse from natal territories at some point after parents stop feeding them, whereas parents remain inside their territory, with some parents even chasing their independent fledglings around natal territories (M. A. Mejías, pers. observ.).

Breeding success and nest threats

Twenty-five of 42 (60%) clutches produced at least one hatchling, and 10 of those 25 (40%) produced at least one fledgling. Breeding success rate (percentage of nests with eggs that fledged at least one chick) was 24% across years. Bermuda Vireos produced one brood per breeding season, although re-nesting was common after nest failure. Following a nest failure, breeding pairs commenced construction of a new nest within 1–22 days (6 ± 5 days, $N = 30$ nests). Pairs never reused nests, but instead, always laid replacement clutches in a new nest.

I identified 4 causes of nest failure at 27 nests with eggs or nestlings: predation ($N = 16$, 59%), nest collapse (7, 26%), nest abandonment (3, 11%), and nestlings falling out (1, 4%). The Argentine ant was responsible for 5 (33%) predation events involving eggs and nestlings, as evidenced by ant swarms covering the nest, eggs, or dead nestlings. Kiskadees and rats were likely responsible for predation events where predators were unconfirmed. I saw a kiskadee divebomb a brooding vireo with newly hatched chicks, and this nest was found destroyed

approximately 3 days later. Similarly, I often saw rats directly beneath or above vireo nests a few days before naked nestlings disappeared. Throughout all these stages, adults defended nests, eggs, and nestlings from threats, both animal and human intruders, with scolding calls, active chasing, and divebombing.

Discussion

This is the first detailed account of the nesting behaviour of *Vireo griseus bermudianus*. The Bermuda Vireo uses several nest tree species, and has a relatively long and asynchronous breeding season, due in part to multiple nest attempts following predation by introduced predators. My observations revealed that its nesting habits are largely congruent with the *Vireo* genus.

I found large variation in pair bond duration. Some pairs were together for less than one year and others for multiple years, although I only confirmed multi-year breeding by one banded pair. While data on vireonid pair duration is scant, Morton et al. (2010) observed several within-year divorces among Blue-headed Vireos (*Vireo solitarius*), with no indication of pairs lasting multiple seasons. Black-capped Vireos (*V. atricapilla*), however, apparently have longer pair durations, with some surviving 3 consecutive seasons (Graber 1961). My maximum pair duration of 4 years was higher than those reported for either species. Pair duration might be more stable in Bermuda than in North America because Bermuda Vireos are non-migratory, thus, these pairs never leave territories vacant or risk mortality with long-distance movements. Interestingly, all recorded divorces in Blue-headed Vireos involved females disappearing from their mate's territories (Morton et al. 2010). These findings are similar with my observations of Bermuda

Vireos, where the end of pair bonds involved males remaining in their territories and females departing and visiting nearby unpaired males in neighbouring territories. In Bermuda, one female was involved in sequentially monogamous pair bonds with 4 neighbouring males from February to May 2017; female Blue-headed Vireos also behaved in this manner (Morton et al. 2010). Sexual selection (Andersson 1994) may favour a vireonid breeding system in which it is costly for males, as the competing sex, to relinquish their territories and associated resources, but beneficial for females, as the choosy sex, to desert.

Vireo breeding phenology varies across species, although most studies are biased towards northern species. More specifically, temperate vireos have short breeding seasons that generally span April – August (Bell's Vireo, *V. bellii*, Nolan 1960; Blue-headed Vireo, Marvil and Cruz 1989; Red-eyed Vireo, *V. olivaceus*, Robinson 1981; Philadelphia Vireo, *V. philadelphicus*; Robinson 1981; Plumbeous Vireo, *V. plumbeus*, DeMarco et al. 2000; Cassin's Vireo, *V. cassinii*; Hedley 2019). Shorter breeding season can facilitate greater breeding stage synchrony among nesting vireos (Morton et al. 1998). For example, the incubation periods of Philadelphia Vireo (Robinson 1981) and Warbling Vireo (*V. gilvus*; Smith et al. 2004) occur mostly in June and July, respectively, whereas the incubation period of *bermudianus* spans 5 months. Temperate vireos have a narrower window of favourable weather for breeding prior to their southern migration. In contrast, tropical and subtropical regions have protracted warmer periods, which may allow these non-migratory vireos to have longer breeding seasons.

Despite differences in breeding phenology and parental care among *Vireo* species, the genus nevertheless shows overall conservatism in duration of each breeding stage: nest building (5–8 days; Graber 1961, James 1997), incubation (14–17 days; Gómez-Montes and Moreno 2008, Morton et al. 2010), and nestlings care (12–13 days; Graber 1961, James 1999). Data on

the duration of fledgling care are unavailable for most vireonids. Fledgling care lasts ca. 28 days in San Andreas Vireo (*V. caribaeus*; Gómez-Montes and Moreno 2008) and 44–52 days in Black-capped Vireo (Graber 1961, Grzybowski 1991). Similarly, the Bermuda Vireo cares for fledglings for 26–57 days. Grzybowski (1991) noted that *Vireo* fledgling care lasts longer than in most passerines; this, coupled with high nest failure, might partially explain why Bermuda Vireos only rear one brood annually.

Bermuda Vireo nests were generally vireonine in structure: open pensile cup made of fibrous strips of plant, lichen, and garbage, suspended from a horizontal forked branch by “basket handles” (Brewer et al. 2019). Despite all *Vireo* nests being cup-shaped, the outer wall and nest lining reflect the respective habitat being used (Lapergola et al. 2012, Brewer et al. 2019, Mejías et al. 2020). Bermuda Vireos used strips of bark and palm fronds, mosses, lichen (*Ramalina denticulata*), and garbage bits (especially polyfill stuffing) to form the outside wall, and lined nests with reddish-brown straw fibers from old leaf bases of either Bermuda Palmetto or Chinese fan Palm. Typical of its generalist nature (Mejías and Nol 2020), Bermuda Vireos built their nests in 14 tree species, most of which were introduced. A similar diversity of 11 tree species was used by a mainland population of White-eyed Vireos (Peake and Ritchison 1998). Similarly, Bermuda Vireos built their nests at an average height of 2.5 m above the ground, whereas the mean height of nests in continental, White-eyed Vireos is 0.8–1.5 m (Peake and Ritchison 1998, Conkling 2010).

Crowell and Rothstein (1981) reported that Bermuda Vireos produce an average clutch size of 2 eggs and 3-egg clutches in the North American race. However, my larger sample size shows that clutch size in Bermuda Vireos is like that of continental *V. griseus* (2–4 eggs, average of 3; Ritchison et al. 2019). Bermuda Vireo nestlings are naked at hatching, with the first feather

sheaths appearing by 3 days, feathers bursting around day 6, and nestlings fully feathered by day 9, just prior to fledging; my observations matched growth patterns described for other vireo species (Brewer et al., 2019). At least two patterns of parental contribution occur in *Vireo* species. In one, males do not assist with nest building or incubation, but help with nestling care (Rust 1920, Barlow and Rice 1977). In the other, both sexes contribute to all phases of the breeding cycle (Ritchison et al. 2019); the Bermuda Vireo belongs to the second group. Brewer et al. (2019) noted the tendency of female Black-capped Vireos to rear their fledglings beyond natal territories, with the males largely feeding in their own territories, as I found for Bermuda Vireos.

Most nesting attempts in Bermuda were unsuccessful. Nesting pairs in Bermuda made as many as four nest attempts, although Puerto Rican Vireo (*Vireo latimeri*) pairs made up to six attempts (Faaborg et al. 1997); such data appears unavailable for other vireonids. In Bermuda, only 50% (42 of 84) of nests that were initiated lead to eggs being produced. Nest predation from introduced predators (16 of 42 nests with at least eggs) and nest collapse (7 of 42 nests) were the primary and secondary causes of nest failures in the Bermuda Vireo, respectively. Low breeding success is common among mainland and island vireos (Graber 1961, Tossas 2008, Siepielski et al. 2001, Kovar et al. 2018, Ritchison et al. 2019). Brood parasitism from the native Brown-headed Cowbird (*Molothrus ater*) on the mainland (Pitelka and Koestner 1942, Graber 1961, Marvil and Cruz 1989) and from introduced Shiny Cowbirds (*M. bonariensis*) in the Caribbean (Wiley 1985, Woodworth 1995) is the primary cause of nesting failure in said populations. Neither of these brood parasites is present on Bermuda during the breeding season (Amos 1991). Nest collapse in Puerto Rican Vireos was attributed to the additional weight of cowbird nestlings (Woodworth 1997). I hypothesize that nest collapse in Bermuda was due to a lack of sufficient

nest binding material, specifically, the durable silk of golden silk orb-weavers (*Trichonephila clavipes*) that was historically a common component of Bermuda Vireo nests (D. B. Wingate, pers. comm). I found no evidence of golden silk in any of the nests I observed, possibly because this arachnid is no longer as abundant.

The Bermuda subspecies of White-eyed Vireo is of significant, local conservation importance because it is the last endemic terrestrial bird that breeds on the archipelago. Presently, introduced predators are the primary cause of nest failure. However, the Bermuda Vireo's ability to live in introduced vegetation (Mejías and Nol 2020), to use diverse materials for constructing nests, and to make multiple breeding attempts (this study) likely offsets their poor nesting success. Future studies should analyze the Bermuda Christmas Bird Count Data, comprising 74 years of single-day island-wide bird surveys, and then estimate population trends of the Bermuda Vireo. A long-term mark-recapture study would also be useful in determining survival and recruitment of this subspecies. Lastly, research can test whether choice of native versus introduced nest trees, or the percent composition of plant, litter, and spider silk in the nest, especially of *T. clavipes*, affect whether Bermuda Vireo nests fall apart.

Co-authorship Statement

I am the primary author of Chapter 4; this produced a manuscript which was coauthored by David Wilson. I came up with the research idea, did all the fieldwork (with the help of my parents), summarized and quantified the data, wrote the entire manuscript, and produced all figures. David Wilson provided feedback which improved the manuscript.

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Tables

Table 4.1. Estimates of pair bond duration of 18 nesting pairs of colour-banded Bermuda Vireos between 2016–2021. Colour bands (B = Blue, G = Green, LB = Light Blue, O=Orange, P = Pink, PU = Purple, R = Red, W = White, Y= Yellow) on the left and right leg are separated by a slash. A status of “Unknown” indicates a pair whose duration together was not followed closely. In all but one pair (Male O/BG and Female O/LBY), the end of a pair bond involved males remaining in their original territory and the females deserting, which often involved pairing with other males in neighbouring territories; note female RWG/ was paired with 4 different males throughout the 2017 breeding season. Once separated, previously paired individuals never re-paired. Dates and pairing durations are conservative because it is possible that birds were paired before the “First Seen Paired” date and that they remained paired after the 'Last Seen Paired' date.

Pair (Male; Female)	First Seen Paired	Last Seen Paired (Days Paired)	Known Number of Nest Attempts
BO/; B/	11 October 2016	19 July 2017 (282)	2
YG/; OPB/	29 January 2017	18 May 2017 (110)	1
R/; OY/	20 February 2017	26 May 2018 (461)	1
BBP/; RWG/	20 February 2017	20 February 2017 (1)	0
BBP/; BWG/	24 May 2017	11 February 2021 (1360)	5
BBP/; OY/GW	26 May 2021	17 November 2021 (176)	2

O/; BWO/	14 April 2017	19 May 2017 (36)	1
O/; PUBW/	26 May 2018	1 August 2019 (433)	Unknown
O/P; O/BO	3 May 2019	14 June 2019 (43)	2
O/YB; BWPB/	25 April 2019	26 December 2019 (246)	4
OPU/; RWG/	1 March 2017	17 March 2017 (17)	Unknown
G/LB; R/LB	4 August 2017	7 August 2018 (369)	1
GY/; RWG/	14 April 2017	20 April 2017 (7)	1
BWB/; RWG/	28 April 2017	21 st May 2017 (24)	1
G/Y; Y/Y	13 July 2017	28 July 2018 (381)	Unknown
O/BG; O/LBY	20 December 2018	16 August 2019 (240)	4
/RP; O/BY	26 April 2019	4 May 2019 (9)	1
O/OP; O/LB	19 December 2018	7 June 2019 (171)	2

Table 4.2. Fate of Bermuda White-eyed Vireo nests. Number of nests observed from 2016–2021 is shown for each nest status or event. For one nest that was depredated in 2019, I was unsure whether it contained eggs or nestlings at the time it depredated.

Nest Status or Event	2016	2017	2018	2019	2020	2021	Total
Nests initiated	2	30	9	36	2	5	84
Nests completed	2	27	9	34	1	3	76
Total nests abandoned	0	5	0	12	0	2	19
Total nests fell apart	0	11	0	10	0	0	21
Nest fell with eggs/nestlings	0	5	0	2	0	0	7
Nest fate unknown	2	6	7	5	1	1	22
Nests with eggs	Unknown	17	3	18	1	3	42
Known clutch size	Unknown	12	1	7	0	1	21
Nests with nestlings	Unknown	8	3	10	1	3	25
Clutch abandoned	Unknown	1	0	2	0	0	3
Clutch predation	Unknown	2	0	2	0	0	4
Nestling predation	Unknown	3	0	7	0	1	11
Nestling fell out of nest	0	1	0	0	0	0	1

Nests produced fledglings	Unknown	3	2	3	1	1	10
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Table 4.3. The duration of breeding stages in Bermuda White-eyed Vireos, 2016–2021; results are based on stages that were completed and observed in their entirety. N is the number of nests or events.

Breeding Stage	Minimum (Days)	Maximum (Days)	$\bar{x} \pm SD$ Days	N
Nest Building	2	12	5 ± 3 days	13
Incubation	12	16	14 ± 2 days	11
Nestling Care	9	14	11 ± 2 days	6
Fledgling Care	26	57	41 ± 12 days	5

Figures

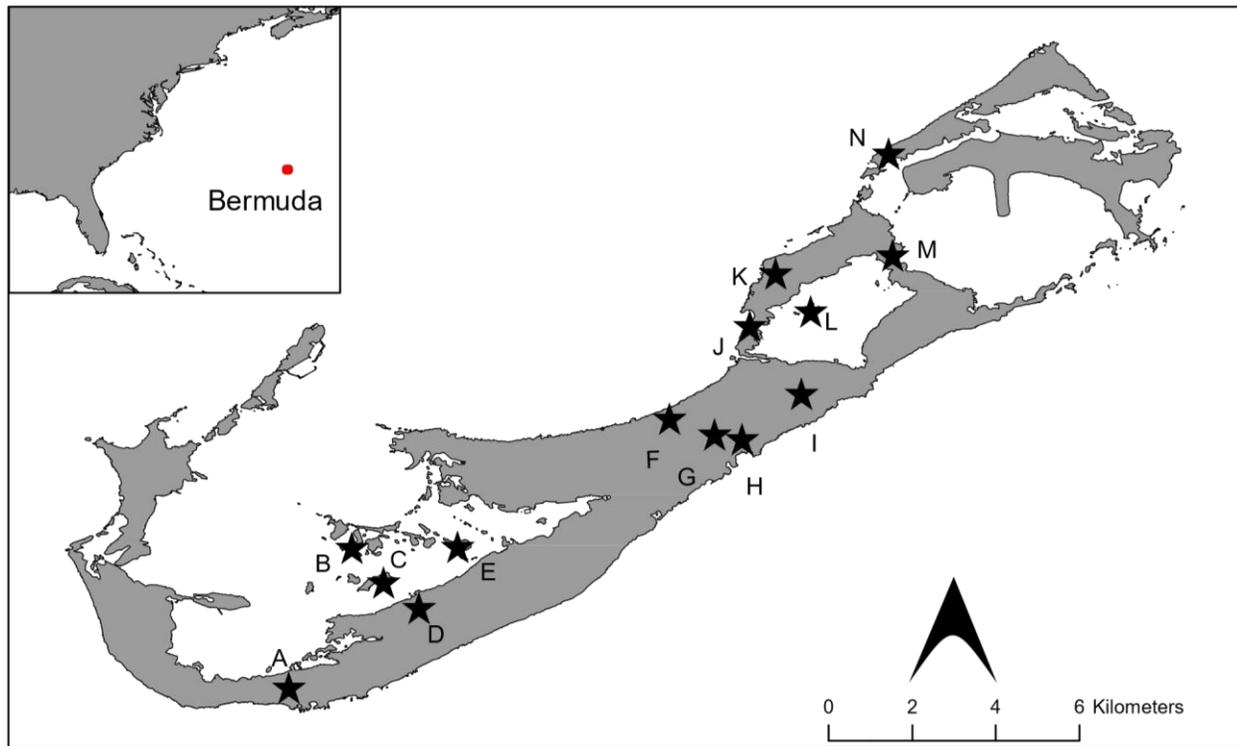


Figure 4.1. A map of the Bermuda archipelago depicting all sites (“stars”) where nesting and breeding behaviour of Bermuda Vireos was observed, 2016–2021: A: Seymour’s Pond (N = 1 nest), B: Gamma Island (0); C: Darrel’s Island (2); D: Elm Lodge (1); E: Hinson’s Island (3); F: Oceanview Golf Course (1); G: Brighton Plant Nursery (1); H: Devonshire Bay (1); I: Spittal Pond (29); J: Shelly Bay Railway Trail (1); K: Radnor Road/Shelly Hall Condos (2); L: Trunk Island (1), M: Blue Hole Park/Tom Moore’s Tavern (2), and N: Ferry Reach/Lover’s Lake (38). The inset map depicts the position of Bermuda relative to the eastern seaboard of North America.



Figure 4.2. A colour-banded male Bermuda White-eyed Vireo. Photograph by Andrea Webb.

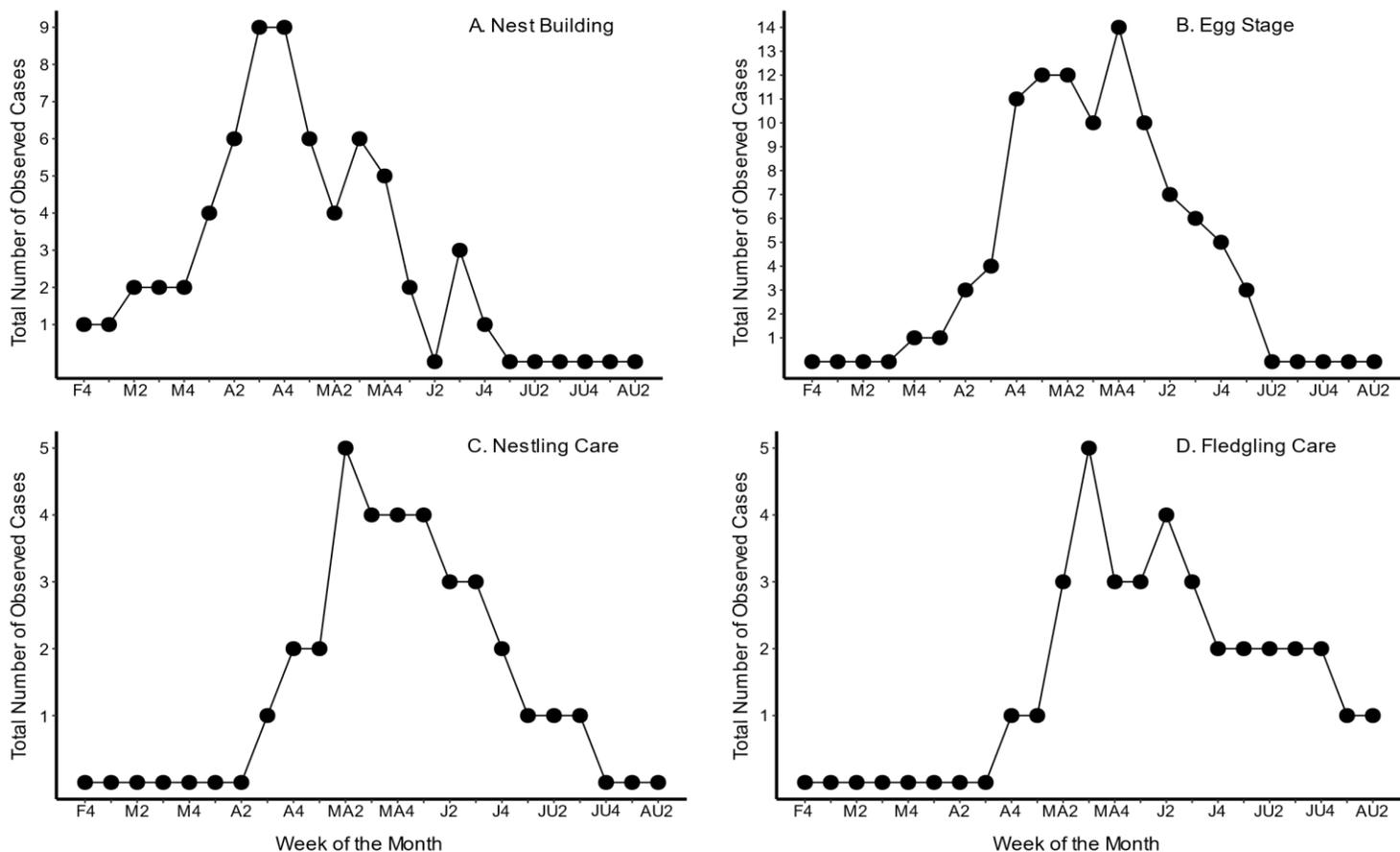


Figure 4.3. Breeding phenology of Bermuda Vireos. The number of nests observed in each breeding stage is shown for each week between February – August during the 2016–2021 breeding seasons. Some nests were observed in the same stage over multiple weeks, and thus contributed to multiple datapoints within the breeding stage panel. Because the number of days in each month varied from 28–31, I included any days beyond the 28th day of the month in week 4. Month abbreviations are as follows: F = February, M = March, A = April, MA = May, J = June, JU = July, and AU = August. Note that the final observation of fledgling care in the second week of August corresponds to a single pair whose fledgling care period ended that week.



Figure 4.4. From left to right, photographs show the progression of nest building in allspice (*Pimenta dioica*) for a breeding pair of Bermuda White-eyed Vireos. Photos were taken on days 0, 3, and 10 of nest construction between 21–31 March 2017. Photographs by Miguel Mejías.



Figure 4.5. A Bermuda White-eyed Vireo (left) and a 3-egg clutch inside a nest cup (right); clutches of up to 4 eggs occur in this subspecies. Both the pensile nest hanging from a forked branch and the small, white eggs with brown speckling and blotching are typical of vireonids. Photographs by Jorge Sanchez (left) and Miguel Mejías (right).



Figure 4.6. Photographs showing the developmental stages, from top left to bottom right, of the same Bermuda White-eyed Vireo nestlings. Note the gradual change from naked and blind hatchlings to feathered nestlings with open eyes. Photographs were taken on days 0 (hatch day), 3, 6, and 9 (fledging day), between 21–30 April 2017. Photographs by Miguel Mejías.

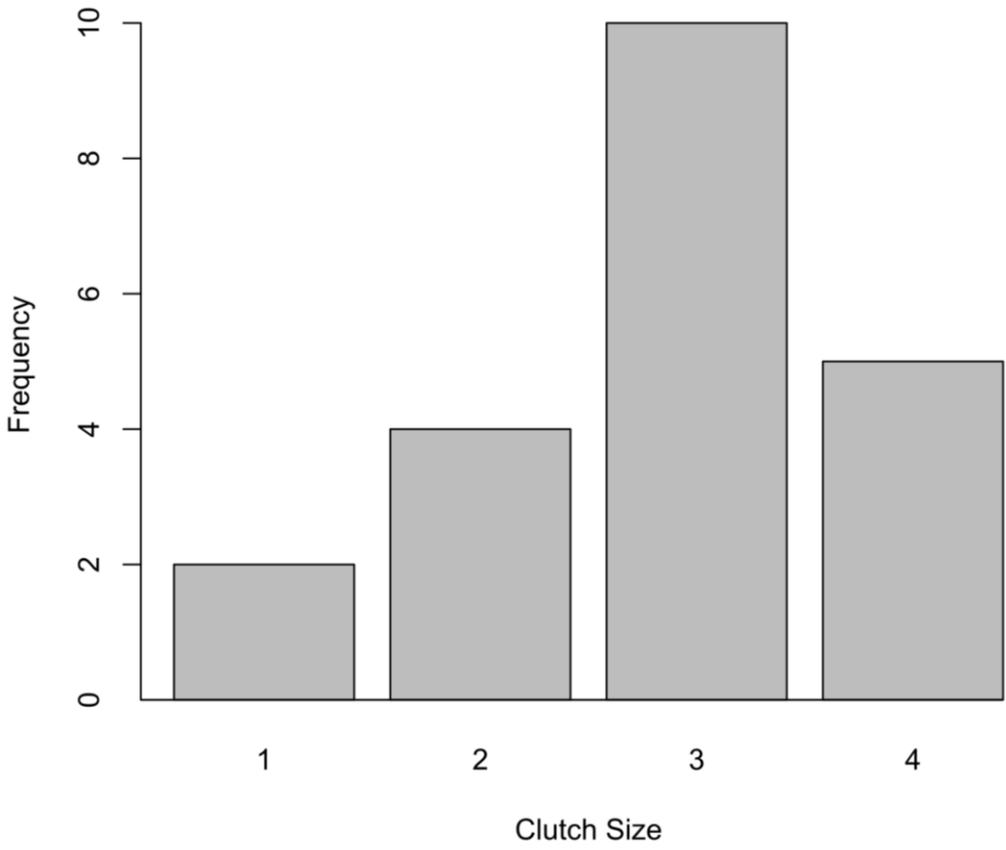


Figure 4.7. Frequency distribution of Bermuda White-eyed Vireo clutch sizes; clutch sizes of 1 and 3 were least and most common among the archipelago, respectively.

Chapter 5:
The relationships of breeding stage to daytime singing behaviour and choice
of song perch height in Bermuda White-eyed Vireos (*Vireo griseus*
bermudianus*)

**This Chapter is the outcome of joint research with D. Wilson*

Abstract – Bird song is crucial for attracting mates and defending territories, but different types of song or different singing behaviours may be involved in acquiring or maintaining each resource. Male songbirds may adjust when and where they sing, depending on their breeding stage. However, such relationships remain untested in several avian taxa. Here, I studied male Bermuda White-eyed Vireos (*Vireo griseus bermudianus*), a passerine with two distinct song types (discrete and rambling), to test the mate attraction, territory defence, and nesting stage hypotheses. I compare song rate and song perch height among different stages of the breeding season and during the non-breeding season. I found that male vireos produce both song types during the breeding and non-breeding seasons, suggesting dual functionality. Singing rate did not differ between the two seasons, but, within the breeding season, males without nesting duties had significantly higher song rates than males with nesting duties. Song rate was lowest during the nestling stage, which coincided with the highest rate of nest predation. Song perch height was higher during the breeding season versus non-breeding season, among males without nesting duties compared to males with nesting duties, and when males produced discrete songs rather than rambling songs. My findings suggest that male vireos may increase their conspicuousness to prospecting females by increasing singing rate and song perch height, and that they sing during the breeding and non-breeding seasons to defend year-round territories. Collectively, my study supports the mate attraction and territory defence hypotheses of bird song and suggests that Bermuda White-eyed Vireos adjust their singing rate in response to nest predation risk.

Introduction

Bird song is diverse among species, yet also varies within species (Rose et al. 2022). One hypothesis for this intraspecific variation is that song serves multiple functions, including territory defence, where males sing to announce occupancy of utilized space (Szymkowiak and Kuczyński 2017, Mejías et al. 2021, Wheeldon et al. 2021) and mate attraction, where males sing to attract females (Kroodsma 1984, Catchpole and Slater 2003, Sockman et al. 2005). In some species that produce multiple song types, different acoustic displays appear to have different intended receivers (Spector 1991, Demko et al. 2013, Janes et al. 2017). In several genera of New World warblers (Parulidae) for example, structurally complex songs among males tend to be sung later in the breeding season and exchanged with rival males, whereas songs that are simple in structure and stereotyped among males are sung primarily in the presence of females early in the breeding season (Ficken and Ficken 1962, Staicer 1989, Janes et al. 2017). These findings suggests that one type of song is instrumental for male-male competition and the other for female attraction, and therefore could drive the observed structural variability in avian songs.

Avian singing behaviour has been shown to change with breeding status, and these observations have laid the foundation for several hypotheses. For example, during their breeding season, Krebs (1977) showed that male Great Tits (*Parus major*) that were removed from their territories and replaced with speakers broadcasting either song or silent controls differed significantly in conspecific intrusion rates: trespassing was higher among silent controls compared to speakers broadcasting conspecific songs. This finding provided strong support for the territory defence hypothesis. In line with the mate attraction hypothesis, vocal output can also be higher among unpaired males than paired males (Staicer et al. 2006, Liu and Kroodsma 2007), with bachelor males singing at higher rates at dawn (e.g., Savannah Sparrows, *Passerculus*

sandwichensis; Moran et al. 2019) or males reducing daytime song once paired (e.g., Chipping Sparrows, *Spizella passerine*; Liu and Kroodsma 2007). Among paired males, nesting stage might also influence singing rate. Predation, the most significant cause of nest failure in songbirds, can be affected by the vocal displays of parents and offspring (Ricklefs 1969, McDonald et al. 2009; Haff et al. 2015). Parents singing near the nest can reveal nest locations to eavesdropping predators, which may explain why some male birds sing less frequently when approaching or sitting on nests (Nice 1930, Bolsinger 2000, Chiver et al. 2007). According to the nesting stage hypothesis, the risk of nest predation changes with nesting stage and are highest during nestling care (Morton et al. 1993, Burhans et al. 2002). The cost of nest failure may also increase with later nesting stages because parents have invested more and have less time remaining to re-nest (Slagsvold 1984, Verhulst and Nilsson 2008). Under the nesting stage hypothesis, birds may assess these risks and reduce their singing when the costs of nest loss are highest, like during the nestling stage.

Breeding stage can also affect song perch height, which is an important component of singing behaviour. During the breeding season, many songbirds use elevated song perches (Castrale 1983, Rodenhouse and Best 1983, Hallworth et al. 2008), yet, despite decades of such observations, few studies have tested for a relationship between breeding stage and song perch height. Some studies have focused on the consequences of song perch choice on song transmission (Mathevon et al. 2005, Barker and Mennill 2009, Mennill et al. 2009), predation risk (Duncan and Bednekoff 2006, Campos et al. 2009), and foraging success (Greig-Smith 1983, Guilfoyle et al. 2002). While these factors undoubtedly influence song perch height among breeding birds, singing from higher perches can also increase the probability of a male being detected by a prospecting female (Petit et al. 1988, Beck and George 2000, Hallworth et al.

2008). In Chipping Sparrows, song perches are higher among unpaired males than paired males, consistent with the hypothesis that males adjust their song perch height according to their breeding stage and whether they are actively seeking a mate (Liu and Kroodsma 2007).

The White-eyed Vireo (*Vireo griseus*) is a small songbird inhabiting shrublands and thickets in the southeastern United States. Its primary songs, sung only by males, are described as fast and robotic in delivery (Adkisson and Conner 1978, Borror 1987), and two distinctive song types are recognized (Bradley 1980). The discrete song is short (ca. 1 s) and comprises highly modulated elements, including chips, buzzes, and whistles delivered in a fixed sequence; individual males have at least 10 discrete song variants in their repertoires (Borror 1987). The rambling song is a long (up to ca. 10 s) warble comprising discrete song elements and harsh scolding elements delivered in an unpredictable sequence and at a faster rate than for discrete songs. Previous observations suggest that discrete songs function primarily in territory defence and rambling songs function primarily in female interactions (Bradley 1980), though their usage among seasons, breeding stages, and social contexts remains unquantified. A non-migratory subspecies known as the Bermuda White-eyed Vireo (*V. g. bermudianus*) or “*chick-of-the-village*” (hereafter Bermuda Vireo) is endemic to the Bermuda archipelago (Bangs and Bradlee 1901, Mejías et al. 2021). Like the continental form, it sings both discrete and rambling songs.

The overall goal of this study is to gain insight into the function of song in male Bermuda Vireos by testing whether song production and song perch height are associated with breeding stage. First, I quantify the number of discrete and rambling songs used during breeding and non-breeding seasons. Since Bermuda Vireos maintain year-round territories, a song type that is confined to the breeding season suggests that it is used primarily for acquiring a mate, whereas a song type that is produced consistently throughout the year suggests that it functions in territory

defence. Second, using the mate attraction and nest predation hypotheses, I test whether vocal output is associated with a male's nesting status. I predict that males without nesting duties sing more than males with nesting duties (i.e., mate attraction), and that song rate is lowest during the nestling care stage when nests experience the highest predation risk (Morton et al. 1993, Burhans et al. 2002). Third, I test whether song perch height is related to breeding stage. Since singing from higher perches should increase the probability that a male is detected by a distant prospecting female (Liu and Kroodsma 2007), I predict that song perches are higher during the breeding season than the non-breeding season, for males without nesting duties than for males with nesting duties, and when males sing rambling songs rather than discrete songs (Bradley 1980).

Methods

Study site and study species

Bermuda is a remote island (32°18'N, 64°47'W) formed from fossilized, calcareous shell-sand (Verrill 1902). It lies in the western North Atlantic Ocean, roughly 965 km off the eastern seaboard of the United States. The island is low-lying, yet hilly (0 m – 76 m, mean: 38 m) with a subtropical climate (18 – 27.5°C). Sunshine and light winds occur from April-September, whereas rain and gales are more prevalent during the winter months (Amos 1991). My general approach was to monitor male Bermuda Vireos intensively over a prolonged period (see description of data collection below) in order to observe changes in their singing behaviour across multiple breeding stages of the breeding season as well as during the non-breeding season. I collected data at Spittal Pond Nature Reserve (60 acres) and Ferry Reach Park (64 acres)

(Figure 5.1). Present-day wooded habitat in Bermuda is dominated by invasive secondary forest (Mejías and Nol 2020, Mejías and Mejías 2020). Trees in my study sites included introduced Brazilian pepper (*Schinus terebinthifolius*), casuarina (*Casuarina equisetifolia*), and fiddlewood (*Citharexylum spinosum*), and a few native trees such as southern hackberry (*Celtis laevigata*), bay grape (*Coccoloba uvifera*), and Bermuda cedar (*Juniperus bermudiana*).

In May 2018, January 2019, and April 2019, I captured 10 male and 4 female vireos along walking trails at Spittal Pond and Ferry Reach Park by luring them into mist nests using conspecific song recordings. I determined their sex by observing whether vireos sang discrete song (known only in males; Bradley 1980) as they approached the mist net or during follow-up observations (see details below). Female response to target netting playbacks was weak and I was unable to capture the remaining females associated with captured males. I fitted captured birds with an aluminum Porzana identification band on one leg and either one or two plastic colour bands on the other leg. I released banded birds at their point of capture within 10 min. To increase my sample size, I also added 4 additional colour-banded vireos (2 males and 2 females) living at my two study sites. In total, I had 12 colour-banded males that served as my focal subjects (Spittal Pond: 7 males; Ferry Point Park: 5 males). All colour-banded birds comprised 6 breeding pairs throughout the study period. I developed estimates for the territorial boundaries of subjects by opportunistically following it for 1–2 hours on several days throughout the banding period as males roamed their territories. I marked the GPS coordinates of several perches with a handheld GPS unit (model: Garmin eTrex® 10, approximately 3 m accuracy; Garmin International, Inc., Olathe, KS, U.S.A). During the 2019– 2020 study period, I refined the whereabouts of territory boundaries for each individual (see details in “Singing behaviour”). In general, territories during the 2018–2019 banding period were the same as the 2019– 2020 study

period. Two exceptions occurred: (1) one male I captured in January 2019, for which I had yet to map his original territory, had, by April 2019, taken over a territory previously occupied by another male, approximately 100 m away, and (2) a male I banded in December 2018 had disappeared by December 2019.

Singing behaviour

I collected recordings of daytime (0700–1200 h) singing behaviour of the 12 male birds during the species' breeding season (April – August 2019), which included breeding activities such as nest building and caring for fledglings (see below). Of these 12 males, 11 also were recorded during the following non-breeding season (December 2019 – January 2020); one male had disappeared and was not recorded in the latter period. Researchers often record birds either just before or at dawn (Bolsinger 2000, Dolan et al. 2007, MacDonald and Islam 2021) when passerine song typically peaks (Staicer et al. 1996, Dabelsteen and Mathevon 2002). I recorded vireos during the morning hours after sunrise for two reasons. First, Bermuda Vireos sing discrete and rambling songs starting at dawn with song rate remaining high until ca. 1500 h (M. Mejías unpub. data). Second, the extremely dense vegetation created by exotic trees reduced visibility before sunrise and made it difficult to locate, follow, and record birds at that time.

As part of my sampling regime, I visited one of my two sites each day during favorable weather (i.e., no rain and little to no wind), alternating between sites each day. In total, I visited the Ferry Reach Park site 41 times during the breeding season and 5 times during the nonbreeding season. I visited the Spittal Pond site 44 times during the breeding season and 7 times during the nonbreeding season. While at a site, I recorded each male at the site during a

separate 15-minute recording session throughout the morning. My goal was to obtain unbiased estimates of singing behaviour from each male across multiple breeding stages. I therefore randomized the order in which I recorded subjects each day, thus reducing the risk of recording certain males or males at certain breeding stages at the same time each day.

Upon arriving at a subject's territory, I searched for him for ≤ 15 min. If I found him, I waited 2 min before commencing recording. The delay was important because I sometimes located subjects by hearing them sing. Since my goal was to obtain unbiased estimates of singing behaviour, including estimates of daily song production, waiting for 2 min reduced the risk of biasing my recording sessions towards periods of time when the male was known to be singing. If I did not see or hear the focal male after 15 min, I stood in the approximate center of his territory, waited an additional 2 min, and commenced recording. Given the relatively small size of Bermuda Vireo territories (0.25 ha), their loud songs, and my familiarity with the song repertoires of the 12 birds, I was confident that I would readily detect and locate the focal male anywhere in the territory if he began vocalizing after the start of the recording. If a vireo began singing from what we thought was the inside of the territory, I immediately approached him while recording. If I located the singing male and confirmed that he was our focal subject, I included in my analysis all the songs recorded throughout the 15-min session, including those acquired before visually locating him. In the rare instances when the singing male I located was not the focal subject (e.g., a neighbour), I aborted the recording session and repeated it later that day.

I recorded subjects throughout their 15-min session with a digital audio recorder (Marantz PMD661 MK II Professional recorder; WAVE format; 44.1 kHz; 16 bits) and a shotgun microphone (Sennheiser ME66 with K6 power module; super cardioid pickup pattern;

40–20,000 Hz frequency response (± 2.5 dB)) fitted with a foam windscreen. Recordings were made by following the subject at a minimum distance of 5 m while pointing the microphone directly at him (or towards the source of the songs if I had not yet located him). For each song produced while the subject was visible, I spoke into the microphone and estimated his song perch height above the ground visually (estimated accuracy ± 1 m); very few trees across Bermuda Vireo territories were > 10 m; all height estimates were made by the same person. I noted any periods in which I lost visual contact with the subject, but always continued recording until the 15-min session expired. After recording, if confirmed visually, I used a handheld GPS unit (Garmin eTrex® 0, ~ 3 m accuracy; Garmin International, Inc., Olathe, KS, USA) to mark general singing localities (separated by ≥ 5 m) of each male, per trial. I used ≥ 5 m because Bermuda vireos move continuously through their territories with short (~ 1 -3 feet) flutter hops interspersed occasionally by longer (up to a few metres) loping flights (M. Mejías pers. observations).

In May 2021, I returned to my sites and measured the heights of the two tallest trees in each subject's territory to allow comparisons between the heights of used song perches and the heights of the tallest perches available to my subjects. I estimated maximum tree height by extending a Telescopic Fibreglass Mast Heavy Duty Pole (model MFJ-1916; maximum height = 10 m) alongside the selected tree and visually estimating (estimated accuracy ± 1 m) the remaining height of the tree above the fully extended pole. Estimates of the heights of used song perches and the tallest trees were conducted by the same individual.

Breeding stage

During the breeding season, I revisited subjects in the afternoons (1300–1700 h) to document their breeding activities. I spent a maximum of 30 min searching for a given male, and usually found them on account of their loud vocalizations and small territories. I followed located males at a minimum distance of 5 m and categorized them into one of six breeding stages: (1) no nesting duties, (2) nest building, (3) egg stage, (4) nestling care, (5) fledgling care, or (6) non-breeding (non-breeding status was assumed for all males between December 2019 and January 2020; Mejías 2021). I defined nest building as the stage when vireos are locating and adding materials to a nesting branch until a nest is completed. I defined the egg stage as the period after nest completion, where the vireos are engaged in activities associated with egg laying and incubation; the egg stage ultimately terminates at hatching. Nestling care is the stage when nestlings are seen inside the nest cup and the parents are actively feeding or brooding them. Fledgling care is the stage when the young are outside the nest and being fed by their parents.

Because I was unable to colour-band every female, it was difficult to determine reliably whether subjects were paired or unpaired, as has been done in some previous studies (Liu and Kroodsma 2007, Brunner and Pasinelli 2010). Separation between male-female pairs occur in my study system. For example, one of my subjects that was seen with his colour-banded mate was subsequently observed in his territory 4 days later building a new nest with a new unbanded female, and his original colour-banded mate was never seen again. For males that were paired to unbanded females, a temporary absence of the female (i.e., 2-3 weeks) therefore could mean that she was replaced by another unbanded female following a period in which the male was unpaired, or it could simply mean that I was unable to find her and that they had remained paired

throughout. To avoid the ambiguity of assigning paired and unpaired status, I instead categorized males as with or without “nesting duties.” During the breeding season, I considered males to have nesting duties if they were engaged in nest building, the egg stage, nestling care, or fledgling feeding, and to be without nesting duties if they were without a female or not engaged in any of the above nesting behaviours with their partner. I often could not see a female accompanying a male that was without nesting duties, but I refrain from categorizing such males as “unpaired.”

Nests were located during afternoon sessions by following vireos as they carried nest material or food for nestlings. Bermuda Vireos rear one brood per season, with pairs making up to five breeding attempts if previous attempts fail (Mejías et al. 2021). For this reason, some of the focal males experienced the same nesting stage multiple times throughout the breeding season. Whenever possible, I identified the causes of nest failure. The black rat (*Rattus rattus*), Great Kiskadee (*Pitangus sulphuratus*), and Argentine ant (*Linepithema humile*) were abundant across study sites and are known predators of Bermuda Vireo eggs and chicks (Mejías 2021, Chapter 4). Predation from ants was obvious because swarms would take several days to consume eggs and nestlings. Kiskadee or rat predation was not observed directly, but these potential predators were often observed near nests a few days before the sudden and complete disappearance of eggs or nestlings. Once a nest was inactive due to fledging or predation, I recorded its location with the same GPS unit. I imported the GPS coordinates of all nest and singing localities into ArcMap 10.7.1 and used the “generate near table” to measure the distances (1 m resolution) between each subject's nest and its various singing locations.

Quantifying singing behaviour

I generated waveforms and spectrograms (Hamming window, FFT = 512 samples, 87.5% overlap) for all 15 min recordings using Raven Pro sound analysis software (v1.5; Cornell Laboratory of Ornithology, Ithaca, NY). On each spectrogram, I drew cursor boxes (hereafter, “annotated”) around vireo songs that were visible on the spectrogram and waveform (i.e., clear pulses in amplitude). In some instances, songs from non-focal males could be seen and heard in the background of the recording, but these were easily distinguished from the subject's songs either because they were relatively faint or because they did not match the known vocal repertoire of the subject. I defined songs as vocalizations comprising one or more elements, where elements of the same song are separated by < 0.5 s and those of different songs are separated by ≥ 0.5 s (Mejías et al. 2020, Mejías et al. 2021). My song definition did not hinder my ability to identify discrete songs and rambling songs (Figure 5.2), as defined by Bradley (1980: Figures 1B, 2A, B, and C). In total, I annotated 17,682 vireo songs from 430 15-min recordings. To make my 15-min measure of vocal activity comparable to previous studies, I multiplied the number of discrete and rambling songs in each recording session by four to obtain hourly rates.

Statistical analyses

I tested the hypotheses that male singing rate and song perch height vary in relation to breeding stage and song type using R (3.5.2; R Development Core Team, R Foundation of Statistical Computing, Vienna, Austria). Firstly, to test whether the number of discrete songs per hour varied among the six breeding stages, I used a generalized linear mixed model (*lme4* package; Bates et al. 2015). I included the discrete song rate from a given recording session as the response variable, the breeding stage (i.e., no nesting duties, nest building, egg stage, nestling care, fledgling care, non-breeding) observed that same day as a fixed factor, and subject identity

(1–12) as a random effect to account for possible dependencies among multiple recording sessions of the same male. The response was modeled with a negative binomial distribution and log link. The overall statistical significance of breeding stage was tested using the *Anova* function of the *car* package (Fox and Weisberg 2019). Post-hoc linear contrasts of estimated marginal means (*emmeans* package; Lenth 2021) were then used to compare discrete song rate between the breeding (i.e., mean of no nesting duties, nest building, incubation, nestling care, and fledgling care) and non-breeding seasons, between the no nest duty and nest duty stages (i.e., mean of nest building, incubation, nestling care, and fledgling care) of the breeding season, and between the nestling care stage and the other nesting stages (i.e., mean of nest building, incubation, and fledgling care). I could not repeat this analysis on rambling song because preliminary inspection of the data revealed that only 5% of all songs were rambling song, thus precluding reliable estimates of rambling song rates from our short recording sessions. For example, only 11 rambling songs were detected during the entire nestling care period.

Secondly, to test whether song perch height was associated with breeding stage or song type, I used a generalized linear mixed model. The song perch height (m) of each song was included as the dependent variable, with breeding stage and song type as fixed factors, and recording session (1–32) nested within subject identity (1–12) as a random effect to account for possible dependencies among multiple perch heights estimated from the same recording session of the same male. The response was modeled using a Poisson distribution with log link. After testing the overall significance of breeding stage and song type, post-hoc linear contrasts of estimated marginal means were used to compare song perch height between the breeding and non-breeding seasons and between the no nest duty and nest duty stages of the breeding season. Results were considered statistically significant where $P < 0.05$. I used the DHARMA package

(Hartig 2020) to validate the two statistical models. Its diagnostic tests, combined with visual inspection of scaled residual plots, indicated adequate model fit. I also simulated the responses of each model and compared the simulated data to the original data by overlaying semi-transparent histograms of each; in all cases, I found strong agreement between the simulated data and the original data.

Results

Recording effort and a general description of singing behaviour

Bermuda Vireos were vocally conspicuous amongst the island's woodland avifauna. Counter-singing among neighbouring males was common and I observed this at both the edge and interior of a singer's territory. My fieldwork produced 430 15-min recordings across the breeding (April – August 2019; $N = 374$ recordings) and non-breeding seasons (December 2019 – January 2020; 56), equating to 6,450 min. I obtained more recordings of focal males during the breeding season (mean \pm SD: 31 ± 3 recordings per male; range: 26–37 recordings; $N = 12$ males) than the non-breeding season (5 ± 0.30 recordings; 5–6 recordings; 11) because my winter residency on the island was limited compared to the summer months. Subjects produced at least one song in 349 (81%) of the 430 recordings. A total of 17,682 vireo songs were detected from the recordings, and, of these, 16,818 (95%) were discrete songs and 864 (5%) were rambling songs. Males produced both song types during the breeding and non-breeding seasons; discrete song rate was fairly constant throughout the breeding and non-breeding season, with the lowest rates recorded in August (Figure 5.3). I note that August also marked the onset of feather

moult in my subjects, where males with missing tail feathers spent more time feeding quietly than singing.

Male Bermuda Vireos used multiple song perches throughout their territories and vocalized at varying distances from their nests. Seldom did males vocalize while either sitting inside the nest cup or while perched on the rim. Occasionally, incubating males sang a couple of discrete songs, with noticeably longer pauses between songs. These were often followed immediately by the female returning to the nest and relieving the male, which then resumed steady bouts of discrete song away from the nest. In general, breeding males used song perches away from the nest (mean \pm SD: 18 ± 18 m; range: 0–86 m). With respect to perch height, males accompanied by a female or engaged in nesting duties often alternated between singing and flutter-hopping amongst understory perches. In contrast, males in the breeding season with no nesting duties usually performed stationary song bouts from exposed canopy perches.

Breeding performance

All 12 males made at least one breeding attempt (3 ± 1 nests; 1–5), but only 3 nests (each from a different male, or 25% of focal males) produced fledglings. In total, I found 34 completed nests across the 12 focal territories. The Argentine ant was responsible for at least 3 nest failures, as evidenced by swarms found devouring known nest contents. Field observations suggest that the black rat and Great Kiskadee also depredated nests (see “Discussion”). I recorded 10 predation events, of which 9 (26%) were of known stages; 2 (6%) during the egg stage and 7 (21%) during nestling care. Additional causes of nest failures of completed nests include nest abandonment ($N = 10$, 29%) and nests falling apart (6, 18%); the entirety of nest fates for 2019 are summarized in Chapter 4

Singing rate in relation to breeding stage

Discrete song rate varied significantly among the six breeding stages (Analysis of Deviance: $\chi^2 = 19.65$, $df = 5$, $P = 0.0015$; Figure 5.4). Post-hoc linear contrasts showed that discrete song rate did not differ between the breeding and non-breeding seasons (estimate \pm SE (log scale): -0.39 ± 1.21 ; $Z = -0.32$, $P = 0.7489$). Within the breeding season, however, discrete song rate was higher for males with no nesting duties than for males with nesting duties (mean of nest building, egg stage, nestling care, and fledgling care; estimate \pm SE (log scale): 2.78 ± 0.81 ; $Z = 3.46$, $P = 0.0005$). Discrete song rate was also lower during nestling care than during other nesting stages (mean of nest building, incubation, and fledgling care; estimate \pm SE (log scale): -2.87 ± 0.99 ; $Z = 2.89$, $P = 0.0039$).

Factors associated with song perch height

I estimated song perch heights for 6,793 of the 17,682 (34%) songs recorded. Males sang from a wide range of perch heights (5 ± 3 m; 1–17 m; Table 5.1, Figure 5.S1), but rarely sang from the tallest available perches (15 ± 4 m; 9–22 m; Table 5.1). Song perch height varied significantly among the six breeding stages (Analysis of Deviance: $\chi^2 = 25.05$, $df = 5$, $P = 0.0001$) and between the two song types ($\chi^2 = 8.01$, $df = 1$, $P = 0.0047$). Post-hoc linear contrasts showed that song perches were significantly higher during the breeding season than during the non-breeding season (estimate \pm SE (log scale): 1.12 ± 0.50 ; $Z = 2.27$, $P = 0.0235$; Figure 5.5A), and significantly higher for breeding males with no nesting duties than for breeding males with nesting duties (estimate \pm SE (log scale): 0.88 ± 0.27 ; $Z = 3.25$, $P = 0.0012$; Figure 5.5B). Song perch height also differed significantly between rambling and discrete songs ($\chi^2 = 8.01$, $df = 1$, P

= 0.0047), with males singing rambling songs from significantly lower perches (estimate \pm SE (log scale): -0.11 ± 0.04 ; $Z = -2.83$, $P = 0.0047$; Figure 5.5C.).

Discussion

I found strong relationships between the singing behaviour of territorial male Bermuda Vireos and their breeding activities. Although the Bermuda Vireo can be heard year-round, my study suggests that males become visually more conspicuous during the breeding season by ascending to higher song perches, before returning to their usual haunts in the understory vegetation for the remainder of the year. Males extensively used discrete songs rather than rambling songs year-round, though discrete song rate did not differ between the breeding and non-breeding seasons. But, during the breeding season, males with nesting duties sang fewer songs than males without nesting duties, and males caring for nestlings produced the fewest songs of all. Song perch height was higher during the breeding season than during the non-breeding season, for breeding males without nesting duties than for breeding males with nesting duties, and when males sang discrete songs rather than rambling songs.

White-eyed Vireos, like several other species in the genus *Vireo*, have a species-typical song and a longer, faster, run-on song termed “discrete song” and “rambling song,” respectively, in the former species (Lawrence 1953; Graber 1961; Nolan 1960; Nolan 1962; James 1978; Bradley 1980; Robinson 1981; Gomez-Montes and Moreno 2008; Hedley 2016). That the production of discrete song did not differ between the breeding and non-breeding seasons, suggests that discrete song functions, at least partially, in year-round territorial defence. Similar patterns of song production have been described for non-migratory tropical birds that also defend

year-round territories (Tobias et al. 2016). The rambling song was generally rare, as it is in continental, White-eyed Vireos (Bradey 1981), and I was unable to compare its rate of production between seasons. Nevertheless, several observations support a territorial defence function. It is produced in the non-breeding season and, compared to discrete songs, was produced lower in canopy, where male-male interactions typically occur (Liu 2004). Although anecdotal, Bermuda Vireos sang rambling songs during several close-quarter countersigning exchanges with neighbouring males that I observed. I note, however, that one male also directed rambling song towards a female moments before copulating with her, suggesting that rambling songs might indeed function in a breeding context too.

Other aspects of my findings provide evidence that Bermuda Vireo song functions in mate attraction. During the breeding season, males without nesting duties usually were unaccompanied by a female and spent this period singing discrete songs at a high rate, whereas males with nesting duties were most often accompanied by a female and were significantly less vocal. Similar singing patterns have been described in Bell's Vireos (*Vireo bellii*; Nolan 1960), Yellow-throated Vireos (James 1984), and Warbling Vireos (*V. gilvus*; Howes-Jones 1985), and for several avian taxa beyond the Vireonidae (Powlesland 1983, Hayes et al. 1986, Staicer et al. 2006, Foote et al. 2017). My findings that song perch height was higher during the breeding season than during the non-breeding season, and higher among breeding males without nesting duties than among breeding males with nesting duties, provides further support that Bermuda Vireo song functions to attract mates. Males with no nesting duties performed lengthy song bouts of discrete song whilst remaining stationary on higher branches in the tree crown, before repeating this behaviour at another elevated and frequently visited perch in the territory. These behaviours have also been described for unmated males in Blue-headed Vireos, Yellow-throated

Vireos, South Island Robins (*Petroica australis*), and Chipping Sparrows (James 1978; Powlesland 1983, Rossel 2001, Liu and Kroodsma 2007); these researchers suggest that singing from elevated perches increases an unmated male's visual conspicuousness to prospecting females. Three anecdotal observations provide further support that singing from elevated perches is a mechanism for attracting prospective females: (1) breeding pairs travelled primarily in the understory, (2) nests were never built in the canopy, but, rather, from forked branches, usually 2–3 meters above the ground, and (3) males often returned to canopy perches after their mate disappeared, typically nest failure. The tendency of males to perform discrete songs from higher song perches than rambling might be because the former signal has a louder amplitude than the latter (Bradley 1980) and may thus transmit over longer distances than rambling songs.

Most of the nest predation in my study occurred during the nestling care stage, which is consistent with the predictions of the nesting stage hypothesis (Morton et al. 1993, Burhans et al. 2002). Given the increased risk of nest predation during nestling care, and the fact that songs can alert predators to nearby nests (Ellison and Ydenberg 2019), it is perhaps not surprising that Bermuda Vireos produced the fewest discrete songs during this time. Similar declines in vocal activity during nestling care, compared to other stages of the nesting cycle, have been documented in species spanning multiple avian families, including House Wren (*Troglodytes aedon*, Wilson and Bart 1985), Yellow-throated and Blue-headed Vireo (James 1999), Golden-cheeked Warbler (Bolsinger 2000), Chipping Sparrow (Liu and Kroodsma 2007), and Common Reed Bunting (*Emberiza schoeniclus*, Brunner and Pasinelli, 2010). My observation of song resurgence during the fledgling stage, following the nestling stage (Figure 5.4), appeared to occur because males often used discrete song to guide fledglings throughout the natal territories and to bring them close after securing a food item. There have been no observations of predation

of adult or fledgling Bermuda Vireos, which spend most of their time in thicket understories. The only account of predation was that of a fledgling Bermuda Vireo becoming trapped in the thick webbing of a Golden silk orb-weaver spider (*Trichonephila clavipes*, Reid 1877). Thus, in addition to its established role in passerine song learning (Nowicki et al. 1998), the increased singing rate of males during fledgling care possibly reflects this low predation risk, further supporting the nesting stage hypothesis.

Future research should attempt to further distinguish the functions of the two main song types used by *Vireo* species, as has been done in the two-category singing system of North American parulids (Spector 1992). The many observational studies that preceded our work not only brought to light the ubiquitous nature of the two-category vireonid song system, but also provide a list of vireonid species that can serve as candidates for hypothesis testing. Future research could also test the effects of feather moult on singing rate. In Bermuda, August marks the peak of feather moult in vireos (M. Mejías pers. obs.), where most adults were seen hastily feeding while missing some or all their tail feathers. Feather moult is one of the most energetically expensive and time-consuming life cycles in birds (Rohwer et al. 2009, Kulaszewicz and Jakubas, 2015), and could also explain the drastic decline of song in August, with males prioritizing intensive foraging over vocalizing, as observed in moulting Blue-headed and Yellow-throated Vireos (James 1999). In conclusion, this study found that male Bermuda Vireos are year-round singers that alter their singing behaviour in relation to breeding stage. My results provide support for the territory defence and mate attraction hypotheses of passerine song, and suggest that nesting birds reduce their production of conspicuous songs when their nests are at the greatest risk of predation.

Co-authorship Statement

I am the primary author of Chapter 5; this produced a manuscript which I coauthored with David Wilson. I developed the key ideas, did all the fieldwork (with the help of my parents), analyze the data (with the help of David Wilson), wrote the entire manuscript, and produced all figures. David Wilson revised earlier drafts of the manuscript and provided field equipment that was funded by his research grant (NSERC Discovery Grant # RGPIN-2015-0376).

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Tables

Table 5.1 Height of song perches used by male Bermuda Vireos during the non-breeding season ($N = 11$ males) and during the breeding season ($N = 12$) when males had no nesting duties or were engaged in nesting duties (nest building, incubation, nestling care, or fledgling care). Shown for each male are the mean (\pm SD), minimum, maximum perch heights observed and sample size, as well as the heights and species of the two tallest trees in his territory. Values in bold indicate the heights of native trees. The asterisk next to one male is to highlight that his maximum song perch height is higher than the tallest trees in his territory; this occurred because maximum tree height was measured after a severe hurricane that destroyed the tallest trees in his territory, whereas song perch height was measured before the hurricane.

Male Colour Band ID	Non-breeding Season (m)	No Nesting Duties (m)	Nesting Duties (m)	Tallest Territory Trees (m)
BlackWhiteBlue	4 ± 0.46 ; 4–5, 8	3 ± 0.74 ; 3–5, 8	4 ± 2.77 ; 1–12, 133	15 ^{CA} ; 20 ^{CA}
BlueBluePink	4 ± 1.17 ; 2–6, 68	5 ± 2.68 ; 1–14, 368	4 ± 1.35 ; 2–6, 96	13 ^{CA} ; 15 ^{CA}
BlueGreen	NA	5 ± 1.79 ; 1–7, 168	4 ± 1.72 ; 1–8, 126	16 ^{CA} ; 18 ^{CA}
BlueRed	2 ± 0.84 ; 1–3, 5	6 ± 2.10 ; 2–9, 63	5 ± 1.99 ; 1–8, 597	10^{SH}; 14^{BC}
GreenOrange	5 ± 0.91 ; 2–7, 121	5 ± 0.93 ; 2–7, 130	5 ± 1.61 ; 1–8, 396	9 ^{FW} ; 11 ^{CA}

GreenRed	3 ± 1.25; 1–5, 43	4 ± 3.71; 1–14, 331	5 ± 2.35; 1–10, 405	18 ^C ; 21 ^C
OrangePurple	4 ± 1.60; 1–6, 42	2 ± 1.41; 1–5, 56	4 ± 2.36; 1–10, 380	14 ^C ; 15 ^C
Pink	2 ± 0.71; 1–3, 8	4 ± 1.32; 1–5, 246	3 ± 1.23; 1–6, 118	11 ^{IL} 13 ^C
Purple*	NA	4 ± 1.87; 1–8, 199	5 ± 3.63; 1–14, 65	10 ^{FW} ; 10 ^{FW}
RedPink	3 ± 1.36; 1–6, 88	8 ± 4.36; 1–17, 1285	4 ± 2.27; 1–12, 128	17 ^C ; 18 ^C
WhiteGreen	NA	9 ± 2.90; 1–14, 701	5 ± 1.69; 1–8, 162	13 ^C ; 15 ^C
YellowBlue	2 ± 1.40; 1–8, 66	3 ± 1.63; 1–12, 46	4 ± 1.70; 1–9, 85	15 ^C ; 22 ^C

Superscript initials correspond to the following tree species: Bermuda Cedar (BC), Casurina (CA), Fiddlewood (FW), Indian Laurel (IL), and Southern Hackberry (SH).

Figures

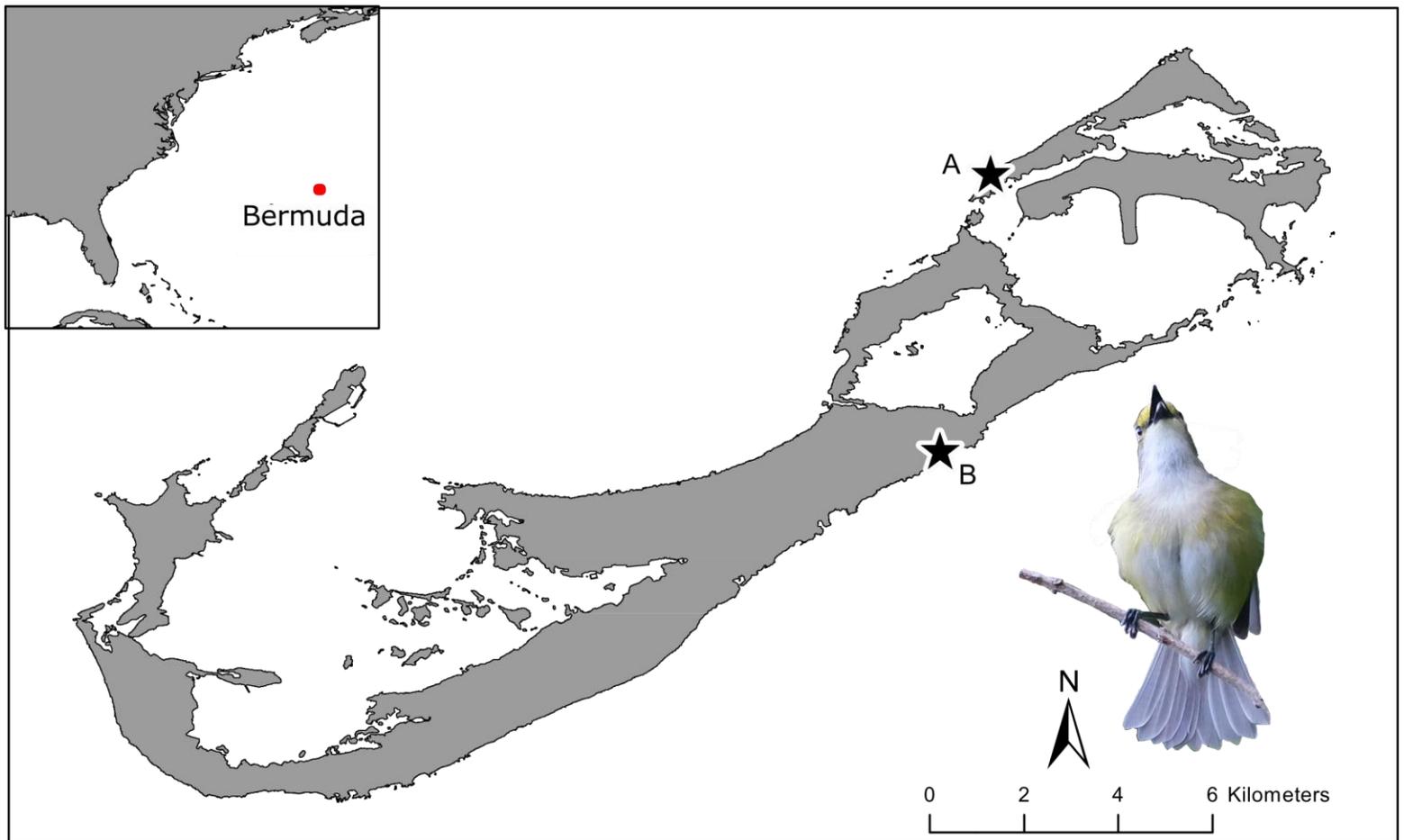


Figure 5.1. Two sites in Bermuda where 12 colour-banded male Bermuda White-eyed Vireos were recorded throughout the breeding and non-breeding seasons: (A) Ferry Reach ($N = 5$ males) and (B) Spittal Pond ($N = 7$). Photograph by Andrea Webb.

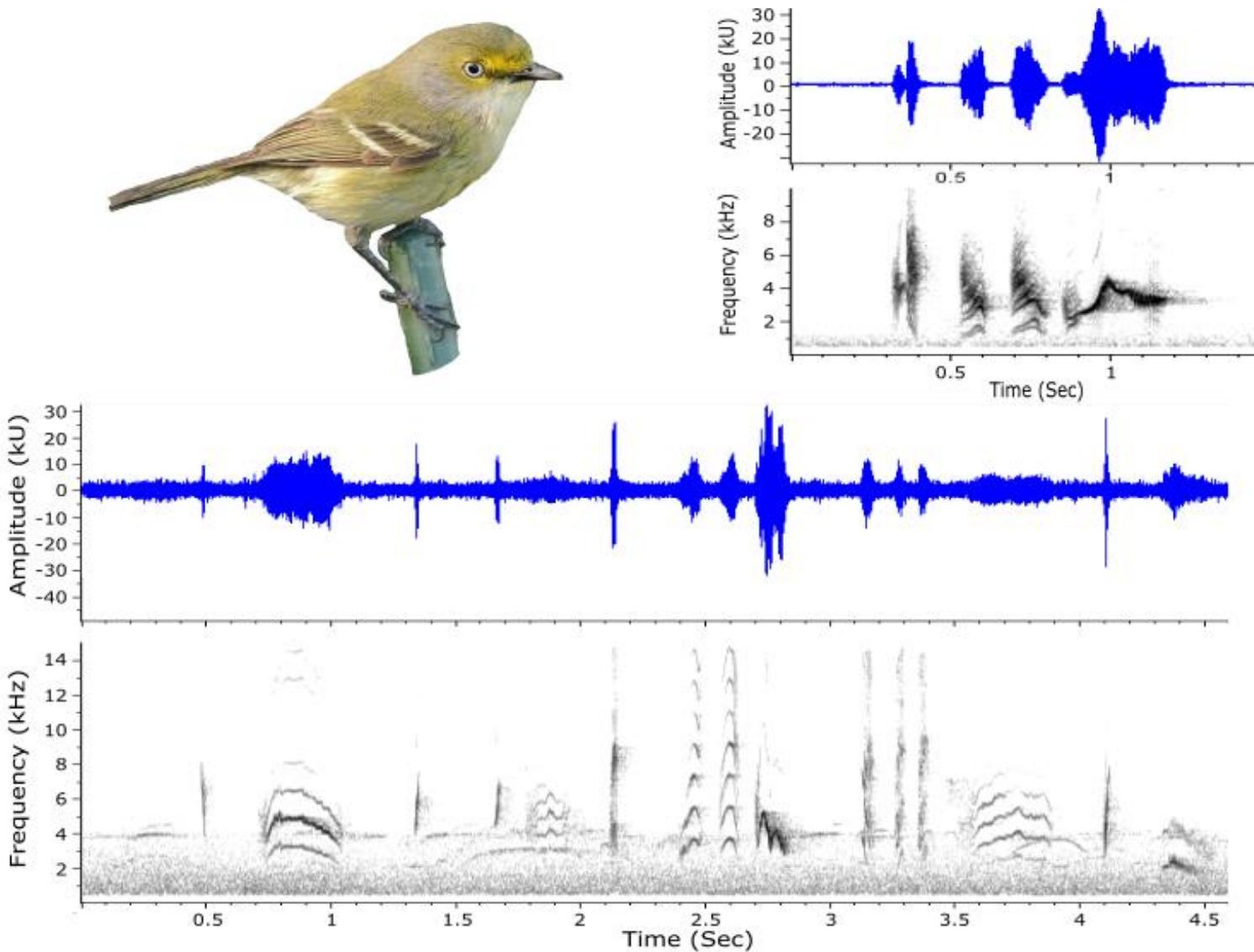


Figure 5.2. Waveforms and spectrograms depicting the two primary vocalizations of male Bermuda White-eyed Vireos: discrete song (top right panels) and rambling song (bottom panels). The discrete song is short (ca. 1 s) and comprises highly modulated elements, including chips, buzzes, and whistles delivered in a fixed sequence; males repeat the same sequence several times before switching to another distinct discrete song type in their repertoire (Bradley 1980). The rambling song is a long (up to ca. 10 s) warble comprising discrete song elements and harsh,

scolding elements delivered in an unpredictable sequence (Bradley 1980). Spectrograms were created using a Hamming window, 512-point fast Fourier transform, and 87.5% overlap.

Photograph by Richard Brewer.

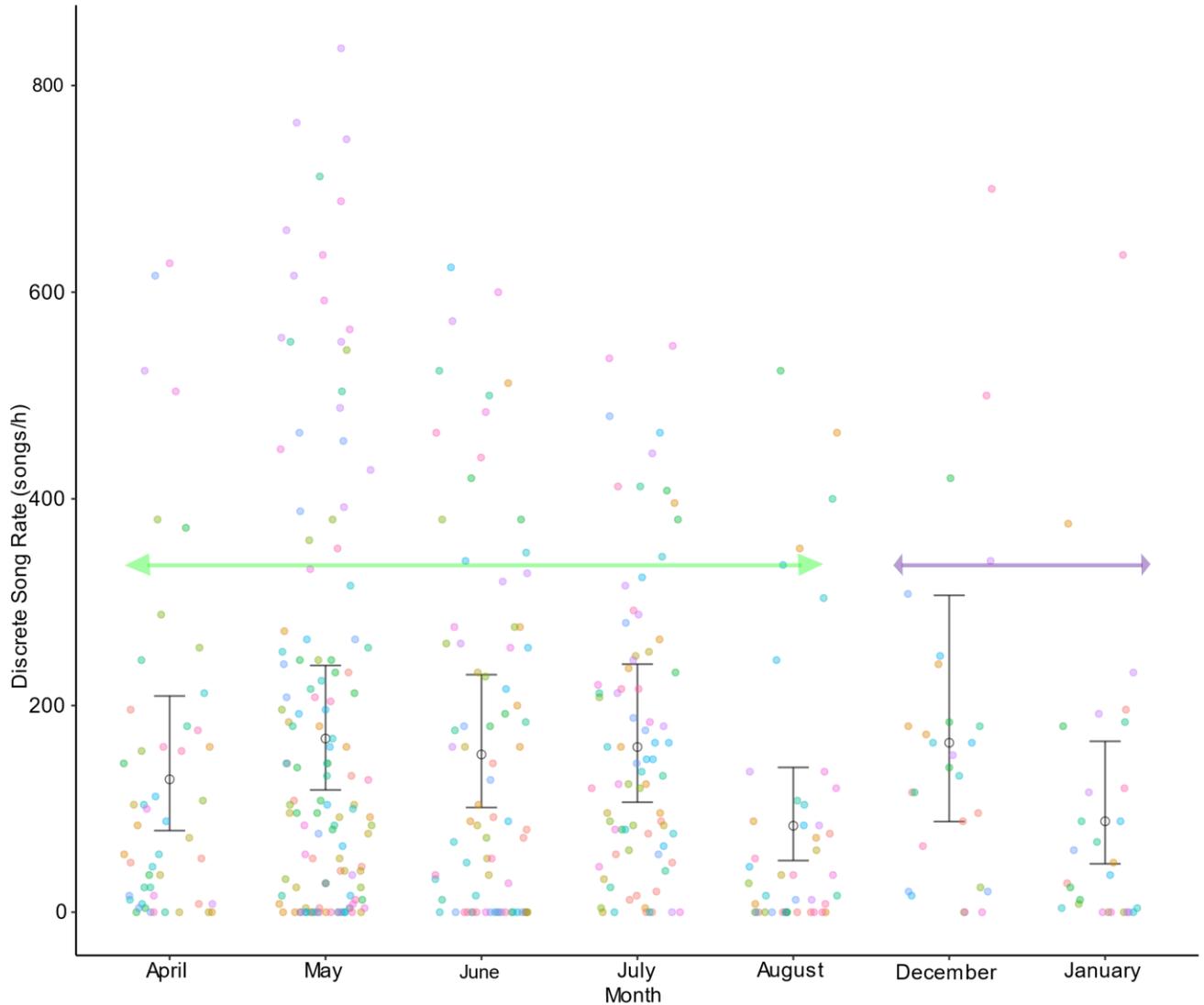


Figure 5.3. Discrete song rate (songs/h) of male Bermuda White-eyed Vireos during the breeding season (April – August; green arrow) and non-breeding season (December –January; purple arrow). Estimated marginal means and 95% confidence intervals derived from a generalized linear mixed model (see text for details) were back-transformed to the original scale and plotted for each month for descriptive purposes and to facilitate planning of future research. Different coloured dots correspond to different colour-banded male Bermuda Vireos recorded during the study.

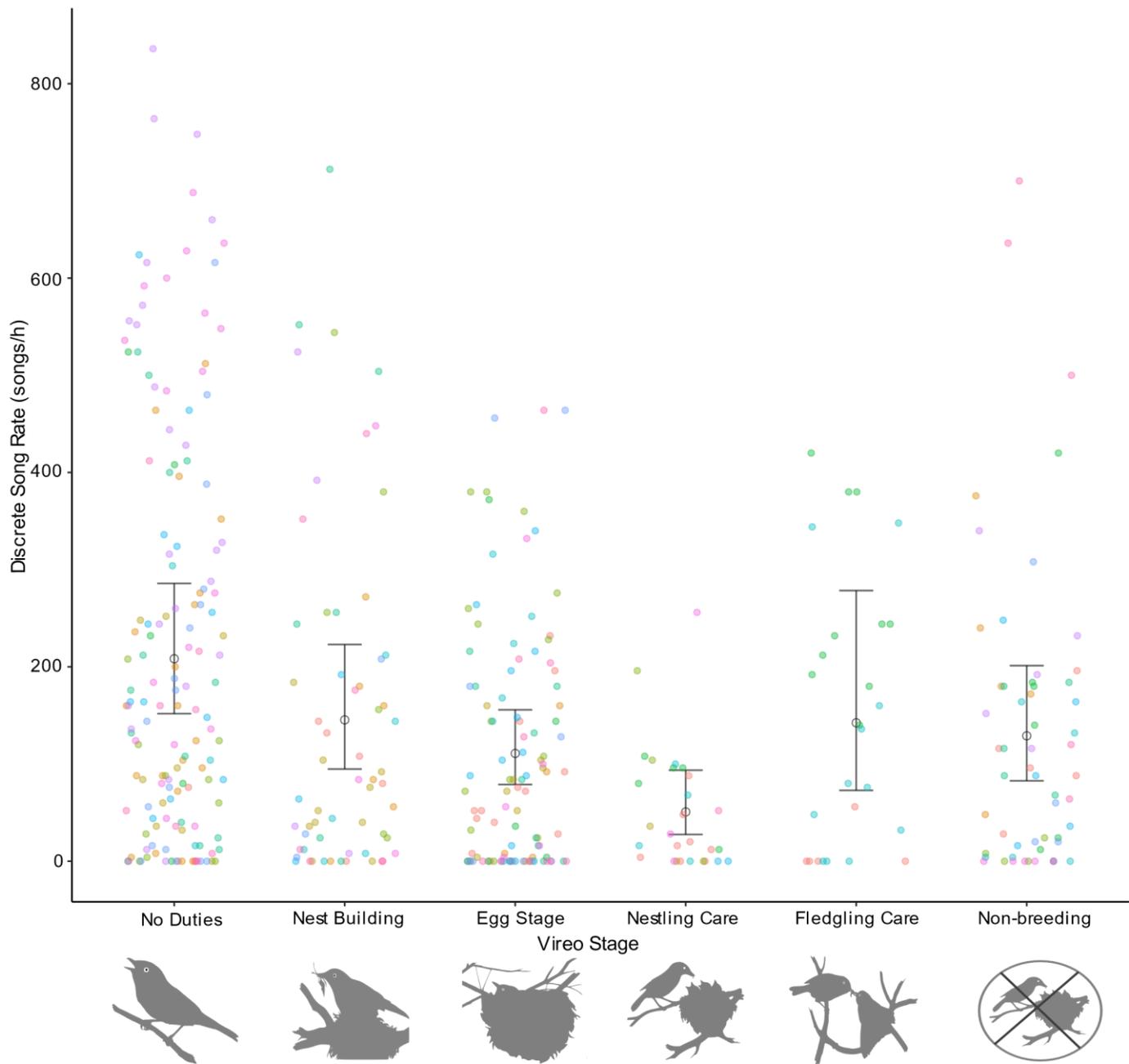


Figure 5.4. Discrete song rate (songs/h) of male Bermuda White-eyed Vireos across six breeding stages: (1) no nesting duties, (2) nest building, (3) egg stage, (4) nestling care, (5) fledgling care, and (6) non-breeding. Estimated marginal means and 95% confidence intervals derived from a generalized linear mixed model (see text for details) were back-transformed to the original scale

and plotted for each breeding stage. Different coloured dots correspond to different colour-banded male Bermuda Vireos recorded during the study. Discrete song rate was highest among males with no nesting duties during the breeding season and lowest for males rearing nestlings. Vireo silhouettes were drawn by Michelle Pasquin.

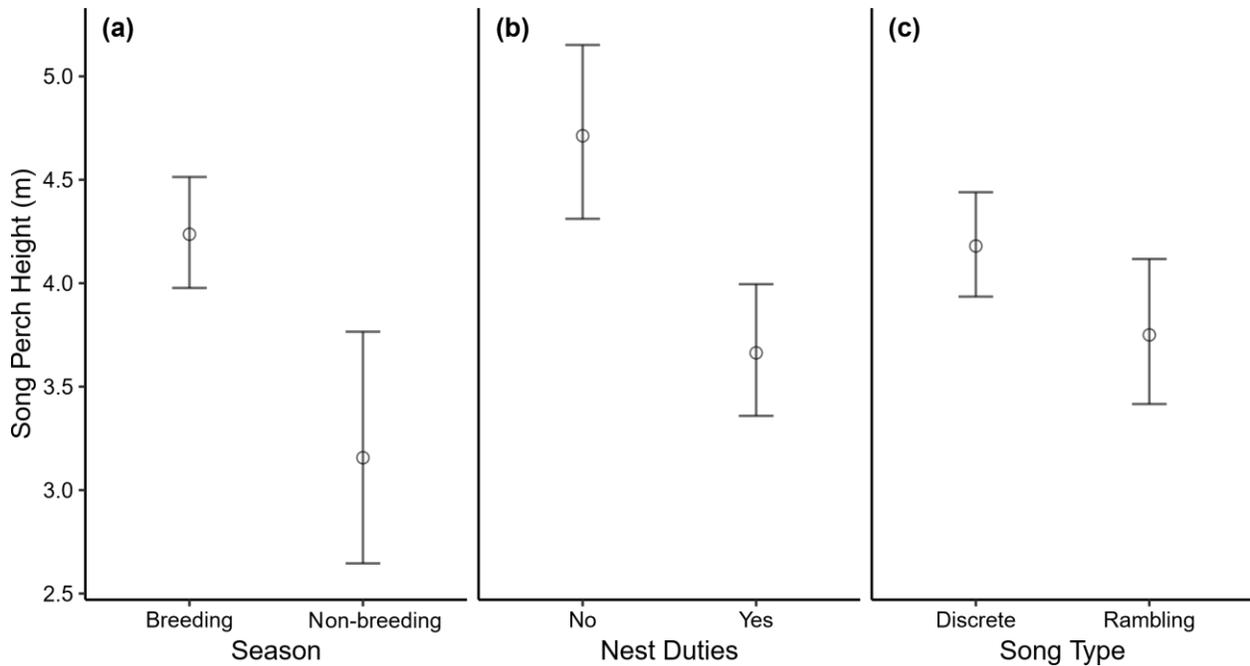


Figure 5.5. Song perch height (m) of male Bermuda White-eyed Vireos across season (a; breeding and non-breeding seasons), nesting duties during the breeding season (b; no and yes), and song types (discrete and rambling songs). Estimated marginal means and 95% confidence intervals derived from a generalized linear mixed model (see text for details) were back-transformed to the original scale and plotted for all three categories. Note that the full range of song perch heights are not shown in this figure.

Chapter 6:
Concluding Chapter

Thesis Summary

In this doctoral thesis, I studied the vocal and breeding behaviour of Vireonidae, with emphasis on the Bermuda White-eyed Vireo (*Vireo griseus bermudianus*). Using song recordings from online sound libraries, and field recordings and nesting observations from the Bermuda archipelago, I explored factors that shaped vireonid song structure, song perception, as well as song function throughout the Bermuda Vireo nesting cycle. Collectively, my thesis provides new evidence of how temporal and frequency components of vireonid songs could be shaped by common ancestry, habitat structure, and morphology (Chapter 2), and novel insight in how acoustic and phylogenetic similarity in these signals, in the absence of sympatry, could influence song perception (Chapter 3). My research also provides the first detailed account of the breeding biology and nesting threats facing Bermuda White-eyed Vireos, a subspecies that, prior to this research, had been little studied. After thoroughly studying their nesting cycle (Chapter 4), I tested, for the first time, how daytime song rate and song-perch choice by male Bermuda Vireos changed as a function of breeding status (Chapter 5).

Chapter 2 Summary: Relationships of song structure to phylogenetic history, habitat, and morphology in the vireos, greenlets, and allies (Passeriformes: Vireonidae)

My first objective was to explain the diversity in song structure within a large family of passerines, the Vireonidae. More specifically, I tested whether temporal and frequency song traits in vireonid songs are related to their phylogenetic history, habitat structure, bill shape and body size. Song length, minimum and maximum peak frequency, and frequency modulation all conformed to the phylogeny; song structure was more similar among closely related species than among distantly related species. Like song traits, bill shape and body size were most similar among closer relatives than among distant relatives. Although habitat structure was not related to

song structure, morphology emerged as a significant predictor; species with shorter, stouter bills and larger bodies produced songs with lower peak frequencies than species with longer, thinner bills and smaller bodies.

Chapter 3 summary: Territorial responses of Bermuda White-eyed Vireos (Vireo griseus subsp. bermudianus)

After shedding light on the drivers of song structure in Vireonidae, I proceeded to test how this song variation is perceived by the birds themselves, to understand whether these diverse songs are a potential behavioural mechanism that reinforces speciation through reproductive isolation. Using a song playback study, I exposed territorial male Bermuda Vireos, which are allopatric to all members of the Vireonidae, to vireonid songs belonging to closely and distantly related species and measured their vocal and physical responses. This allopatry is important because Bermuda Vireos are unfamiliar with these songs. As I predicted, males produced fewer vocalizations and performed fewer speaker flyovers and speaker approaches in response to the songs of distant versus closer relatives. After finding phylogenetic distance predicted male responses, I then showed that dissimilar sounding vireonid songs also elicited weaker vocal responses and fewer speaker interactions, compared to similar sounding songs, from male receivers.

Chapter 4 summary: Breeding Biology and nesting behaviour of the endemic subspecies of White-eyed Vireo (Vireo griseus bermudianus) on the Bermuda archipelago

Although song is widely recognized as being instrumental to mate attraction in birds, the basic breeding biology of some bird species, and threats these nesters face, are largely unknown. I found this to be the case with the non-migratory Bermuda Vireo. This natural history chapter,

based on six years of nesting observations, revealed that this subspecies has a long (8-month) breeding season and lays clutches of 1–4 eggs in small, cup-shaped nests suspended from forked-branches; pairs make multiple nesting attempts until successful or till the season ends. During their breeding season, both sexes contributed the following amount of time to each nesting stage: nest building (5 ± 3 days; mean \pm SD), incubation (14 ± 2 days), nestling care (11 ± 2 days), and fledgling care (41 ± 12 days). Breeding success, however, was low (40%), with egg and nestling predation from introduced species being the primary contributor to nest failure; nests falling apart also proved to be a common cause of nest failure.

*Chapter 5 summary: The relationships of breeding stage to daytime singing behaviour and choice of song perch height in Bermuda White-eyed Vireos (*Vireo griseus bermudianus*)*

Knowledge of the complete breeding cycle of the Bermuda Vireo allowed me to test hypotheses about the roles of bird song and song perch height in mate attraction and territory defence. This subspecies produces two distinctive song types, discrete song and rambling song, and both were used during the breeding and non-breeding seasons. During the breeding season, males with no nesting duties had significantly higher singing rates than males with nesting duties; the nestling stage, when nest predation was at its highest, coincided with the lowest song production amongst fathers. Finally, male song perch height was significantly higher during the breeding season than during the non-breeding season, amongst males without nesting duties than amongst males with nesting duties, and when males performed discrete song compared to rambling songs.

Thesis Contributions to Ornithology

Chapter 2 implications

My research improves our understanding of the evolution of avian song structure, specifically, in the Vireonidae. Birds in this family produce a large array of song types which include short, monotonous trills, short, modulated whistles, ascending or descending repeats of a single element, and short to long warbles comprising chips, buzzes, and whistles (Brewer et al. 2019). My research found significant phylogenetic signal in vireonid song traits, which means sister species inherit similar song traits through common ancestry, with song similarity becoming more dissimilar as time since divergence increases. I also highlighted specific physical traits of the singer that could impose mechanical constraints on the frequency range sung by vireonids; species with heavier bills and larger bodies produced songs of lower peak frequency, compared to species with smaller bills and smaller bodies that produced songs of higher frequency. While my research contributes to the growing literature on avian song structure being shaped by phylogeny (Sosa-López et al. 2016, Arato and Fitch 2021) and morphology (Podos and Nowicki 2004, Demery et al. 2021), I found that these two factors are not mutually exclusively; I detected significant phylogenetic signal in both bill shape and body size. I concluded that the significant phylogenetic signal in song traits is possibly a consequence of song-constraining morphological traits that also evolve according to phylogenetic history. It is my hope that, as a greater number of robust avian phylogenies are published, more studies of this nature are conducted on other avian families with similar acoustic diversity, to find additional support for the interactions of phylogenetic history and morphology in shaping bird song structure.

Chapter 3 implications

My investigation of avian song perception revealed that male Bermuda Vireos exhibit stronger vocal and physical responses towards the songs of closely related versus distantly related species; the former and latter species sung songs that were more similar and dissimilar to the Bermuda Vireo song, respectively. This suggests that male Bermuda Vireos recognize and react to interspecies variation in song traits carrying phylogenetic signal, rather than to song familiarity due to sympatry, since this subspecies is allopatric with all its vireonid relatives. A male's response to a song can be thought of as a proxy for female responses to said stimuli (Illes and Hall 2006, Seddon and Tobias 2006, Christensen et al. 2010). In other words, heterospecific songs that elicit a strong, territorial response in males could mean that females of that same receiver species might be attracted to, and potentially breed with, that heterospecific species, if they were to meet in secondary contact. However, the Bermuda Vireo is still the only vireonid that breeds on the archipelago. Therefore, this continued isolation should promote further divergence from its vireonid relatives.

Chapter 4 implications

My dissertation also provides the first detailed account of the breeding biology and nesting threats facing the Bermuda Vireo, which was recorded on the island as early the 1800s (Reid 1877). Peake and Ritchison (1998) published the only other paper describing the breeding biology and nesting threats faced by continental, White-eyed Vireos. My thesis revealed that the Bermuda Vireo is a habitat generalist that makes multiple nesting attempts, primarily because of threats that are anthropogenic in origin, with introduced predators causing most nest failures.

Indeed, if the Bermuda Vireo were a habitat specialist, like the juniper-reliant Gray Vireo (*Vireo vicinior*; Harris et al. 2020) or the oak-juniper nesting Black-capped Vireo (*V. atricapilla*; Athrey et al. 2012), it would have undoubtedly struggled to persist following the near full replacement of Bermuda's native woodland with introduced trees (Mejías and Nol 2020). Its status as the last remaining endemic terrestrial species makes it of conservation importance to the island. While my research on breeding behaviour and threats to breeding success allowed several hypotheses related to nesting stage to be tested (Chapter 5), it also provided the foundation for a full management plan for the subspecies (Mejías 2021), which can be found in the appendix of this dissertation.

Chapter 5 implications

My newfound understanding of the breeding phenology of the vociferous Bermuda Vireo allowed me to test whether males change their singing rate with season and breeding stage, and whether these same stages and song type are associated with their choice in song-perch height. Both discrete and rambling songs were sung during the breeding and non-breeding seasons, suggesting this subtropical subspecies practices year-round territory defence like non-migratory, tropical passerines (Demko and Mennill 2019, Szymański et al. 2021). In accordance with the mate attraction hypothesis (Kroodsma and Byers 1991), males in the breeding season that were not engaged in nesting activities with a female had higher song rates than males nesting with a female; song perch height followed the same pattern as song rate, which is congruent with one of the pioneering studies exploring these relationships in breeding Chipping Sparrows (*Spizella passerine*; Liu and Kroodsma 2007). My findings that males also reduced their singing rate during nestling care, the same stage that experienced the highest predation rates, suggests that male vireos may attempt to reduce chick loss by not alerting eavesdropping predators when their

young are most vulnerable. I also found that male Bermuda Vireos used higher song perches when singing their primary vocalization, the discrete song, than when singing their rambling song; whether this is because discrete song has better propagation qualities than rambling song is unclear and beyond the scope of my thesis. While the implications of breeding activities on singing rate have been explored in many passerines, their relationships with song-perch height, in comparison, are much less explored. Nonetheless, my findings suggest that male songbirds may convey their unpaired status to prospecting females by increasing their conspicuousness by both their singing rate and song perch height.

Future Directions

Additional research on Vireonidae nesting biology and phylogeny

While my research highlights the vocal displays the Vireonidae use during the breeding season, as well as the nesting ecology of one subspecies, several basic knowledge gaps warrant filling to further our understanding of this family. Harris et al. (2020) acknowledged that the basic breeding ecology of many North American vireonids remains unknown; this is especially true for vireonids in tropical America, the Caribbean, and Asia. A logical next step would be to study and publish detailed nesting accounts (Chapter 4) of these species that would be of use to researchers interested in vireonid biology and conservation. While Slager et al. (2014) published the most completed phylogeny for the family to date (57% of species represented), efforts should be made to collect, sequence, and publish genetic sequences for the unrepresented vireonids in order to improve and resolve additional relationships in the family. A more complete phylogeny

will make robust, between-species comparisons more possible, whilst controlling for non-independence among species due to common ancestry.

Bermuda Vireo repertoire size and song sharing

My observations of singing Bermuda Vireos revealed that each male has a fixed repertoire of multiple discrete song variants. While studies have quantified the element and song repertoire size of continental White-eyed Vireos (Borror 1987, Bradley 1981), similar studies focused on the Bermuda population are lacking. The structural complexity of White-eyed Vireo songs is an ideal model system to test for relationships between song complexity and resource acquisition, where males with larger and more complex repertoires are predicted to have larger territories (Yasukawa et al. 1980, Aweida 1995) and to attract more females (Catchpole 1987, Byers and Kroodsma 2009). I also observed that neighbouring male Bermuda Vireos shared some of the same songs within their repertoires. This warrants future studies on whether these shared songs are important in neighbour-stranger discrimination, with neighbours being recognized by their shared songs, and strangers by dissimilar songs, an approach that has been used with Song Sparrows (*Melospiza melodia*; Stoddard et al. 1991, Beecher et al. 1996).

Function of two song category system in Bermuda Vireo

Several members of the *Vireo* genus produce a shorter primary song and a longer warble; in the White-eyed Vireo, the primary song is known as “discrete song” and the longer song as “rambling song” (Lawrence 1953; Nolan 1962; Bradley 1980; Robinson 1981; Gomez-Montes and Moreno 2008; Hedley 2016). Despite researchers being aware of these two song types, present day vireo research appears to focus exclusively on discrete song. In Chapter 5, I tried to

understand the function of both song types in the Bermuda Vireo, but my sample size for rambling songs was inadequate for most statistical analyses. Bradley (1981) also found rambling song to be quite rare in continental White-eyed Vireos. Despite my low sample size, Bermuda Vireos sang both song types during the breeding and non-breeding seasons, suggesting they might not function exclusively in mate attraction. The presence of two distinct song types that seem to serve the same function, as opposed to the two distinct song types that male warblers direct towards males and females, is puzzling. Therefore, future studies should identify how ubiquitous this two-song category system is among vireonids and quantify the contexts in which rambling songs are given in order to understand their function. If other vireonids sing rambling songs at rates like the White-eyed Vireo, I recommend that recordists surpass the recording effort I adopted for my doctoral thesis.

Vireonid scolding calls and female vocalizations

Another research avenue that has yet to be taken is testing whether the scolding calls of the Bermuda Vireo could act as an alarm call for woodland songbirds. This subspecies generally produces this call when agitated or threatened, especially from conspecifics, and I have observed both resident and migrant passerines being lured to scolding vireos. Arguably the most familiar example of such calls is the “*chick-a-dee*” call of the Black-capped Chickadees (*Poecile atricapillus*), which also attract heterospecific species (Hurd 1996, Templeton and Greene 2007). Like the chickadee, the Bermuda Vireo can also alter the duty cycle of their scolding calls, either emitting scolds slowly with long pauses in between, or with rapid succession, with minimal silent periods between scolds. Using the Bermuda Vireo call, a researcher could conduct a playback experiment to count the number of heterospecific species lured to the speaker after broadcasting calls of varying duty cycles (Templeton et al. 2005, Wilson and Mennill 2011). I

have also observed a unique vocal display that appears to be limited to female Bermuda Vireos, and might be used by continental White-eyed Vireos, since the former is a subspecies of the latter. To the human ear, it sounds like “*fits-few-fits-few*,” uttered softly and rapidly. I have heard females give this note in several contexts, including when her mate is engaged in close-range discrete song exchanges with a neighbour, or when she is close to the nest; there does not appear to be any published account of female vocalizations in White-eyed Vireos. Morton et al. (1998) mentions distinctive “whinny calls” used by female Blue-headed Vireos during female-female conflict. Nonetheless, like rambling songs, this vocalization is uttered rarely and requires more intensive recordings to understand its function, in order to properly classify it as a song or call.

Measure vulnerability of Bermuda Vireos to potential cowbird parasitism

While my thesis and management plan (Mejías 2021) highlight several local threats faced by nesting Bermuda Vireos, other potential threats require study. For example, several species of North American vireo species, including the North American White-eyed Vireo, are highly susceptible to Brown-headed Cowbird (*Molothrus ater*) nest parasitism (Barber and Martin 1997, Ritchison et al. 2019). While Brown-headed Cowbirds only occur in Bermuda as a rare visitor (Amos 1992), it is always possible for this species, or even the Shiny Cowbird (*Molothrus bonariensis*; Post et al. 1993), to one day breed on the island. Given the current status of the Bermuda Vireo as the last remaining endemic terrestrial bird species on the island, it would be good to assess its vulnerability to brood parasitism, if such a colonization occurs; the vulnerability of mainland vireos to cowbirds suggests the Bermuda subspecies would also be threatened. Some researchers have experimentally parasitized nests of songbird species, either familiar or unfamiliar with the Brown-headed Cowbird, by adding fake eggs to a clutch, and measuring the proportion of nests that were accepted or rejected (Briskie et al. 1992). While such

an experiment only addresses one small aspect of brood parasitism, the vulnerability of continental vireos suggests the Bermuda Vireo is also at risk. Therefore, performing such an experiment with nesting Bermuda Vireos could assist local conservationists with constructing and implementing a management strategy to tackle a potential cowbird colonization in Bermuda.

Conclusions

The Vireonidae are a large family of songbirds with diverse song structure. They were an ideal model family to test a series of hypotheses which improved our understanding of the evolution, structure, and function of avian song. My doctoral thesis provides evidence that common ancestry and morphology are two non-mutually exclusive factors that contribute to structural diversity in bird song, which in turn is perceived by males and used to adjust their response strength, as demonstrated by my playback experiment. My thesis also provides novel information on the breeding cycle and threats of the Bermuda White-eyed Vireo, and how male songbirds alter their singing rate and song perch choice to potentially attract mates, defend territories, and avoid nest predation.

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Supplementary Material

Table 2.S1. Body measurements of 136 museum skins from 49 vireonid species. As stated on specimen IDs, morphological traits were collected from The Field Museum of Natural History (FMNH), American Museum of Natural History (AMNH), Museum of Natural Science at Louisiana State University (LSUMZ), and the Bell Museum at the University of Minnesota (MMNH). All measurements were taken by TSI using a digital caliper (Mitutoyo® model no. 573-721) to measure (± 0.01 mm) bill traits by Baldwin et al. (1931): (1) length of exposed culmen (LEC), (2) length of bill from the anterior margin of the naris to the tip (LBN), (3) width of bill at the anterior margin of the naris (WBN), (4) depth of bill at the anterior margin of the naris (DBN), (5) width of bill at its base (WBB), and (6) depth of bill at its base (DBB). The only exception was the 50th species (i.e., *Vireo Chivi*), because it had not been elevated to species at the time of data collection; instead, I included data on three bill measurements (LEC, WBB, and DBB) for Chivi Vireo from Olson (1994).

Species	Sex	Specimen ID	LEC (mm)	LBN (mm)	WBN (mm)	DBN (mm)	WBB (mm)	DBB (mm)
<i>Cyclarhis gujanensis</i>	M	FMNH 327690	15.96	10.1	5.26	7.48	10.18	9.05
<i>Cyclarhis gujanensis</i>	M	FMNH 24619	15.94	10.05	5.19	8.31	8.54	9.75
<i>Cyclarhis gujanensis</i>	M	FMNH 72559	15.51	10.53	5.4	8.18	8.27	9.23
<i>Cyclarhis nigrirostris</i>	M	LSUMZ 162123	18.41	12.44	5.66	7.71	9.45	9.58
<i>Erpornis zantholeuca</i>	M	FMNH 84944	12.25	8.37	3.45	3.83	5.97	4.44
<i>Erpornis zantholeuca</i>	M	FMNH 84947	11.5	8.47	2.99	3.95	5.11	4.83
<i>Erpornis zantholeuca</i>	M	FMNH 84946	12.02	8.82	3.27	3.97	5.87	4.7
<i>Hylophilus flavipes</i>	M	FMNH 297710	11.83	7.68	3.37	3.93	5.75	4.47
<i>Hylophilus flavipes</i>	M	FMNH 251397	10.12	7.82	3.6	3.72	5.51	4.36
<i>Hylophilus flavipes</i>	M	FMNH 298112	11.77	7.83	3.37	3.69	5.82	4.64
<i>Hylophilus olivaceus</i>	M	LSUMZ 85326	12.37	8.27	3.32	3.79	6.13	4.63
<i>Hylophilus olivaceus</i>	M	LSUMZ 174170	12.5	7.79	3.35	3.79	6.02	5.23
<i>Hylophilus pectoralis</i>	M	LSUMZ 174169	13.04	7.87	3.42	3.95	6.46	4.88
<i>Hylophilus pectoralis</i>	M	LSUMZ 153379	12.22	8.42	3.42	4.03	6.49	4.7
<i>Hylophilus poicilotis</i>	M	FMNH 57831	8.96	5.98	2.85	3.28	4.4	4.21

<i>Hylophilus poicilotis</i>	M	FMNH 267606	9.18	6.96	3.17	3.79	5.19	4.59
<i>Hylophilus poicilotis</i>	M	FMNH 72553	9.71	7.04	3.67	3.64	5.28	4.29
<i>Hylophilus semicinereus</i>	M	LSUMZ 137877	13.67	9.14	3.32	3.89	5.75	4.92
<i>Hylophilus semicinereus</i>	M	LSUMZ 153553	12.53	8.19	3.4	4.41	6.22	5.05
<i>Hylophilus thoracicus</i>	M	FMNH 108543	11.13	7.74	3.46	4.1	5.29	5.44
<i>Hylophilus thoracicus</i>	M	FMNH 108542	11.32	8.02	3.44	3.91	5.34	5.21
<i>Hylophilus thoracicus</i>	M	FMNH 260631	11.57	7.76	3.86	3.73	6.04	4.47
<i>Pachysylvia aurantiifrons</i>	M	AMNH 121026	13.26	9.34	3.51	4.04	6.22	5.29
<i>Pachysylvia aurantiifrons</i>	M	AMNH 121017	13.24	9.4	3.53	3.78	5.97	4.52
<i>Pachysylvia aurantiifrons</i>	M	AMNH 121020	13.23	8.87	3.63	3.73	6.67	5.61
<i>Pachysylvia decurtata</i>	M	LSUMZ 163738	11.26	8.03	3.38	3.39	6.05	4.09
<i>Pachysylvia decurtata</i>	M	LSUMZ 163739	12.62	8.39	3.67	3.75	6.3	4.49
<i>Pachysylvia decurtata</i>	M	LSUMZ 170566	11.81	8.05	3.23	3.49	6.01	4.15
<i>Pachysylvia hypoxantha</i>	M	LSUMZ 52360	12.86	8.99	3.32	4.07	5.12	4.68
<i>Pachysylvia hypoxantha</i>	M	LSUMZ 52362	12.16	8.71	3.5	3.84	5.96	4.62
<i>Pachysylvia hypoxantha</i>	M	LSUMZ 52363	13.22	9.21	3.32	3.81	6.82	4.77
<i>Pachysylvia muscicapina</i>	M	FMNH 330727	13.01	9.61	3.5	3.76	6.8	4.7
<i>Pachysylvia muscicapina</i>	M	FMNH 319899	13.79	9.93	3.79	3.75	6.04	4.78
<i>Pachysylvia muscicapina</i>	M	FMNH 264554	12.15	9.49	3.49	3.77	5.96	5.19
<i>Pachysylvia semibrunnea</i>	M	AMNH 109133	13.21	9.29	3.28	4.17	7.28	5.02
<i>Pachysylvia semibrunnea</i>	M	AMNH 109137	12.08	9	3.26	3.94	6.72	5.25
<i>Pachysylvia semibrunnea</i>	M	AMNH 109135	12.97	9.35	3.15	4.11	6.59	5.33
<i>Pteruthius melanotis</i>	M	FMNH 90914	8.14	5.03	4.5	4.14	6.86	4.2
<i>Pteruthius melanotis</i>	M	FMNH 90919	8.6	5.82	4.06	4.21	6.97	4.22
<i>Pteruthius melanotis</i>	M	FMNH 90917	9.07	6.27	3.77	4.21	6.57	4.5
<i>Pteruthius rufiventer</i>	M	FMNH 75500	15.38	10.05	5.24	6.22	9.42	6.68
<i>Pteruthius rufiventer</i>	M	FMNH 75498	15.33	10.41	5.04	6.49	9.27	6.6
<i>Pteruthius xanthochlorus</i>	M	FMNH 236941	8.31	5.99	4.12	3.82	6.64	4.2
<i>Pteruthius xanthochlorus</i>	M	FMNH 236938	8.28	5.47	3.67	4.36	6.47	4.38
<i>Pteruthius xanthochlorus</i>	M	FMNH 221862	8	5.28	3.72	4.08	6.14	4.03
<i>Tunchiornis ochraceiceps</i>	M	LSUMZ 167617	11.74	8.52	3.23	4.3	5.8	4.91
<i>Tunchiornis ochraceiceps</i>	M	LSUMZ 167619	12.03	8.52	3.58	4.14	6.56	4.81
<i>Tunchiornis ochraceiceps</i>	M	LSUMZ 167622	12.01	8.32	3.34	3.92	5.35	4.79
<i>Vireo altiloquus</i>	M	LSUMZ 145063	15.36	11.12	4.02	5.07	7.24	5.56
<i>Vireo altiloquus</i>	M	LSUMZ 145065	15.58	11.35	4.57	4.82	7.4	5.28
<i>Vireo altiloquus</i>	M	LSUMZ 145066	16.97	11.83	4.25	4.27	7.73	5.22
<i>Vireo atricapilla</i>	M	FMNH 292522	9.23	6.85	3.36	3.28	6.33	3.59
<i>Vireo atricapilla</i>	M	FMNH 292514	8.89	6.38	3.04	3.14	5.52	3.43
<i>Vireo atricapilla</i>	M	FMNH 292520	9.58	6.87	3.17	3.45	6.27	3.94
<i>Vireo bairdi</i>	M	LSUMZ 140319	10.66	7.21	3.93	4.14	6.95	4.53
<i>Vireo bairdi</i>	M	LSUMZ 140321	10.94	7.62	4.08	4.25	7.96	4.48
<i>Vireo bairdi</i>	M	LSUMZ 140322	11.63	7.9	4.26	4.15	7.97	4.34
<i>Vireo bellii</i>	M	FMNH 147628	8.68	6.66	3.69	4.1	5.74	4.43
<i>Vireo bellii</i>	M	FMNH 147631	8.63	6.2	3.4	3.56	5.35	3.92
<i>Vireo bellii</i>	M	FMNH 147645	10.15	7.12	3.19	3.74	6.43	4.07

<i>Vireo brevipennis</i>	M	AMNH 153304	10.02	6.36	3.47	3.56	6.1	3.99
<i>Vireo brevipennis</i>	M	AMNH 153303	9.78	6.59	3.73	3.51	6.84	3.67
<i>Vireo carmioli</i>	M	LSUMZ 138787	9.36	6.19	3.38	3.95	6.54	4.27
<i>Vireo carmioli</i>	M	LSUMZ 138789	8.64	6.28	3.51	3.9	6.11	4.29
<i>Vireo carmioli</i>	M	LSUMZ 154077	9.37	6.62	3.29	4.16	6.36	4.28
<i>Vireo cassinii</i>	M	AMNH 89314	10.66	7.37	3.52	4.09	7.37	4.25
<i>Vireo cassinii</i>	M	AMNH 89318	10.56	7.62	3.72	4.12	6.78	4.34
<i>Vireo cassinii</i>	M	AMNH 89290	11.21	7.86	3.72	4.39	6.88	4.4
<i>Vireo chivi</i>	M	Olson1994	15.6	NA	NA	NA	6.7	4.1
<i>Vireo crassirostris</i>	M	LSUMZ 80077	12.76	8.58	4.22	4.47	6.89	4.85
<i>Vireo crassirostris</i>	M	LSUMZ 81519	12.01	8.28	4.21	4.13	6.57	4.27
<i>Vireo crassirostris</i>	M	LSUMZ 81521	11.6	8.15	3.9	4.29	7.34	4.51
<i>Vireo flavifrons</i>	M	MMNH 15569	10.97	7.97	4.79	4.84	6.55	5.45
<i>Vireo flavifrons</i>	M	MMNH 45465	11.09	8.07	3.94	4.5	7.75	4.83
<i>Vireo flavifrons</i>	M	MMNH 45467	10.21	7.98	4.35	4.44	6.65	4.78
<i>Vireo flavoviridis</i>	M	LSUMZ 178839	14.27	10.53	4.15	4.56	7.7	5.16
<i>Vireo flavoviridis</i>	M	LSUMZ 164317	14.03	10	4.44	4.93	7.96	5.41
<i>Vireo flavoviridis</i>	M	LSUMZ 178128	13.79	9.95	3.97	4.49	7.72	5.03
<i>Vireo gilvus</i>	M	FMNH 434217	10.48	7.84	3.89	3.81	6.32	4.13
<i>Vireo gilvus</i>	M	FMNH 434215	10.67	7.76	3.66	3.53	6.12	3.77
<i>Vireo gilvus</i>	M	FMNH 434214	10.19	7.6	3.66	3.67	6.17	4.12
<i>Vireo griseus</i>	M	FMNH 327631	6.04	3.4	3.73	3.91	5.52	4.27
<i>Vireo griseus</i>	M	FMNH 489076	10.96	6.98	3.48	4.04	5.77	4.63
<i>Vireo griseus</i>	M	FMNH 6123	9.56	6.9	3.43	3.88	5.33	3.95
<i>Vireo huttoni</i>	M	AMNH 89325	10.41	6.58	3.37	3.1	7.07	4.32
<i>Vireo huttoni</i>	M	AMNH 89329	10.01	6.64	3.38	3.53	6.53	3.85
<i>Vireo huttoni</i>	M	AMNH 89330	9.86	6.57	3.25	3.26	5.8	3.83
<i>Vireo hypochryseus</i>	M	FMNH 12698	12.5	8.93	3.97	4.04	6.11	4.37
<i>Vireo hypochryseus</i>	M	FMNH 183479	12.45	8.6	3.92	4.47	5.79	4.99
<i>Vireo latimeri</i>	M	FMNH 25484	9.95	7.39	3.66	3.67	5.86	4.16
<i>Vireo latimeri</i>	M	FMNH 25483	10.79	7.44	3.62	3.82	5.43	4.27
<i>Vireo latimeri</i>	M	FMNH 25480	10.82	7.44	3.69	4.02	5.83	4.48
<i>Vireo leucophrys</i>	M	LSUMZ 170144	11.29	8.37	3.44	3.64	6.44	4.1
<i>Vireo leucophrys</i>	M	LSUMZ 172321	10.27	7.41	3.09	3.92	6.39	4.32
<i>Vireo leucophrys</i>	M	LSUMZ 172322	10.63	7.3	3.42	3.51	5.92	3.8
<i>Vireo magister</i>	M	LSUMZ 68380	15.01	10.14	4.77	4.43	7.73	5.2
<i>Vireo magister</i>	M	LSUMZ 68378	15.53	11.38	3.71	5.08	6.85	5.31
<i>Vireo magister</i>	M	LSUMZ 144941	14.21	10.79	3.51	4.82	7.35	5.01
<i>Vireo modestus</i>	M	FMNH 25494	8.69	6.09	3.24	3.77	5.17	4.53
<i>Vireo modestus</i>	M	FMNH 331131	8.84	5.55	3.4	3.43	6.01	3.4
<i>Vireo modestus</i>	M	FMNH 331130	8.44	5.73	3.22	3.45	6.13	3.77
<i>Vireo nanus</i>	M	LSUMZ 146895	8.19	5.71	3.92	3.08	6.77	3.75
<i>Vireo nanus</i>	M	LSUMZ 144910	8.68	6.08	4.48	3.07	6.96	3.21
<i>Vireo nanus</i>	F	LSUMZ xxxxxx1	8.92	6.42	4.28	3.09	6.85	3.2
<i>Vireo olivaceus</i>	M	FMNH 482928	11.84	8.88	4.24	4.48	6.8	4.77

<i>Vireo olivaceus</i>	M	FMNH 365179	12.79	9.57	4.6	4.77	7.34	5.23
<i>Vireo olivaceus</i>	M	FMNH 466986	12.13	9.04	4.19	4.22	6.43	4.64
<i>Vireo osburni</i>	M	AMNH 505375	13.38	9.15	4.03	5.65	7.52	5.98
<i>Vireo osburni</i>	M	AMNH 505374	13.31	9.32	4.38	5.6	8.71	6.17
<i>Vireo osburni</i>	M	AMNH 505369	13.12	9.16	4.24	5.72	7.3	5.95
<i>Vireo pallens</i>	M	FMNH 470619	12.2	7.36	3.74	3.99	5.96	4.7
<i>Vireo pallens</i>	M	FMNH 111961	9.69	7.46	3.87	4.04	5.86	5.48
<i>Vireo pallens</i>	M	FMNH 111960	8.89	6.68	3.56	3.82	5.82	4.23
<i>Vireo philadelphicus</i>	M	FMNH 392107	8.96	6.53	3.38	3.63	5.5	5.06
<i>Vireo philadelphicus</i>	M	FMNH 495662	8.81	6.67	3.45	3.39	5.65	3.55
<i>Vireo philadelphicus</i>	M	FMNH 382106	9.54	7.42	3.77	3.69	5.4	4.36
<i>Vireo plumbeus</i>	M	FMNH 147796	9.89	7.54	3.72	4.6	5.77	4.63
<i>Vireo plumbeus</i>	M	FMNH 17442	10.55	7.9	4.6	4.81	7.24	5.21
<i>Vireo plumbeus</i>	M	FMNH 147794	11	8.49	4.15	4.92	6.49	5.05
<i>Vireo sclateri</i>	M	AMNH 236993	11.04	7.84	2.81	3.66	5.7	3.99
<i>Vireo sclateri</i>	M	AMNH 236992	11.16	7.69	3.37	3.63	6.14	4.27
<i>Vireo sclateri</i>	M	AMNH 236991	12.1	8.53	3.16	4.34	6.46	5.43
<i>Vireo solitarius</i>	M	FMNH 477581	10.85	7.32	3.62	4.23	6.48	4.56
<i>Vireo solitarius</i>	M	FMNH 481968	10.15	7.19	3.8	4.01	5.96	4.32
<i>Vireo solitarius</i>	M	FMNH 492404	9.95	7.2	3.66	4.23	5.99	4.54
<i>Vireo vicinior</i>	M	FMNH 147617	8.34	6.49	3.71	4.76	6.04	5.3
<i>Vireo vicinior</i>	M	FMNH 175926	8.74	6.52	3.63	4.47	5.79	4.87
<i>Vireo vicinior</i>	M	FMNH 25490	9.29	6.77	4.4	4.99	5.65	5.62
<i>Vireolanius eximius</i>	M	FMNH 261746	16.8	11.16	4.59	6.89	8.33	7.3
<i>Vireolanius leucotis</i>	M	FMNH 474647	15.5	10.94	4.6	5.87	8.37	6.93
<i>Vireolanius leucotis</i>	M	FMNH 262378	16.44	10.68	5.39	6.24	8.01	6.69
<i>Vireolanius leucotis</i>	M	FMNH 120407	15.31	10.03	5.24	6.11	8.33	6.4
<i>Vireolanius melitophrys</i>	M	AMNH 105776	17.8	11.59	5.26	7.2	9.54	8.51
<i>Vireolanius melitophrys</i>	M	AMNH 815494	16.06	10.95	5.16	7.17	10.29	7.71
<i>Vireolanius pulchellus</i>	M	FMNH 119767	17.02	11.45	5.26	6.67	8.89	8.06
<i>Vireolanius pulchellus</i>	M	FMNH 119772	15.88	11.15	5.2	6.39	8.82	7.17
<i>Vireolanius pulchellus</i>	M	FMNH 119770	16.34	10.95	4.81	6.4	8.66	7.6

Table 2.S2. Song measurements from 359 individuals from 51 species of male vireonids. Songs were collected from Macaulay and Xeno-canto libraries. I viewed each recording as a waveform and spectrogram (Hamming window FFT size = 512 samples, 87.5% overlap) using Raven Pro v1.5 sound analysis software (Charif et al. 2010).

Species	Song Library	Recording ID	Song Length (s)	Peak Frequency (5 th Percentile; Hz)	Peak Frequency (95 th Percentile; Hz)	Frequency Modulation (Hz/s)
<i>Hylophilus pectoralis</i>	Macaulay	228225	0.99	2756	3407	8717
<i>Hylophilus pectoralis</i>	Macaulay	117124	1.64	2756	3889	13330
<i>Hylophilus pectoralis</i>	Macaulay	106305	1.44	2498	3618	10359
<i>Hylophilus pectoralis</i>	Macaulay	51872	1.6	2670	3359	7049
<i>Hylophilus pectoralis</i>	Xeno-canto	XC323639	1.18	2756	3359	11239
<i>Hylophilus pectoralis</i>	Xeno-canto	XC297050	1.27	2670	3187	8861
<i>Hylophilus pectoralis</i>	Xeno-canto	XC224406	1.2	2756	3359	9809
<i>Hylophilus pectoralis</i>	Xeno-canto	XC150322	0.96	2929	3445	8918
<i>Hylophilus pectoralis</i>	Xeno-canto	XC115713	1.74	2597	3273	12423
<i>Hylophilus pectoralis</i>	Xeno-canto	XC64561	1.58	2472	3273	10728
<i>Vireo bellii</i>	Xeno-canto	XC34881	1.27	2907	4630	30223

<i>Vireo bellii</i>	Macaulay	188220	1.46	2532	4479	23573
<i>Vireo bellii</i>	Xeno-canto	XC34315	1.19	2929	4772	26600
<i>Vireo bellii</i>	Macaulay	516438	1.48	2575	4479	31031
<i>Vireo bellii</i>	Macaulay	212118	1.17	2885	4802	24955
<i>Vireo bellii</i>	Xeno-canto	XC177883	1.27	1352	4910	50245
<i>Vireo bellii</i>	Macaulay	189254	1.01	2890	4518	29508
<i>Vireo bellii</i>	Macaulay	56857	1.06	2739	4565	32346
<i>Vireo bellii</i>	Xeno-canto	XC178894	1.25	2584	4307	28365
<i>Vireo bellii</i>	Xeno-canto	XC109424	1.22	2240	4126	28970
<i>Cyclarhis nigristrois</i>	Xeno-canto	XC386721	0.86	2067	2786	6114
<i>Cyclarhis nigristrois</i>	Xeno-canto	XC57389	0.84	2153	2756	7177
<i>Cyclarhis nigristrois</i>	Xeno-canto	XC386840	0.91	1891	2670	7064
<i>Cyclarhis nigristrois</i>	Xeno-canto	XC347862	1.01	2326	3187	6170
<i>Cyclarhis nigristrois</i>	Xeno-canto	XC22416	1.07	1667	2726	13617
<i>Cyclarhis nigristrois</i>	Xeno-canto	XC252845	0.91	1723	3015	7421
<i>Cyclarhis nigristrois</i>	Xeno-canto	XC222154	1.27	1912	1912	8951

<i>Cyclarhis nigrirostris</i>	Xeno-canto	XC128606	1.27	1723	2498	8503
<i>Vireo atricapilla</i>	Macaulay	105222	0.55	3140	7235	54312
<i>Vireo atricapilla</i>	Macaulay	188204	0.77	2864	6503	40258
<i>Vireo atricapilla</i>	Macaulay	105505	0.85	2769	5646	37520
<i>Vireo atricapilla</i>	Xeno-canto	XC34845	0.8	2980	6374	43066
<i>Vireo atricapilla</i>	Xeno-canto	XC141418	0.65	2825	4978	30234
<i>Vireo atricapilla</i>	Xeno-canto	XC160976	0.31	3531	5857	31647
<i>Vireo atricapilla</i>	Xeno-canto	XC21738	0.69	2730	4332	26231
<i>Pteruthius melanotis</i>	Macaulay	175326	2.925	2842	4221	24307
<i>Pteruthius melanotis</i>	Xeno-canto	XC290913	2.937	2864	4651	29748
<i>Pteruthius melanotis</i>	Xeno-canto	XC201797	4.005	2929	4828	30669
<i>Pteruthius melanotis</i>	Macaulay	XC19584	2.752	3066	4393	31951
<i>Pteruthius melanotis</i>	Macaulay	175231	0.383	2067	2756	6835
<i>Pteruthius melanotis</i>	Macaulay	53562	0.499	1619	2412	11834
<i>Pteruthius melanotis</i>	Macaulay	221817	0.348	1805	2507	12202
<i>Pteruthius melanotis</i>	Xeno-canto	XC79733	0.395	1723	2412	4443

<i>Vireo altiloquus</i>	Macaulay	188061	0.43	2072	4423	30993
<i>Vireo altiloquus</i>	Macaulay	187079	0.905	2153	4186	30556
<i>Vireo altiloquus</i>	Macaulay	135938	0.847	2067	4074	28280
<i>Vireo altiloquus</i>	Macaulay	133257	0.615	2283	4479	34730
<i>Vireo altiloquus</i>	Macaulay	105336	0.557	2119	3618	29774
<i>Vireo altiloquus</i>	Macaulay	44032	0.871	2119	3704	23924
<i>Vireo altiloquus</i>	Macaulay	38464	0.511	2412	4126	22330
<i>Vireo altiloquus</i>	Macaulay	11702	0.511	2412	4823	33761
<i>Vireo altiloquus</i>	Macaulay	133214	0.569	2240	4221	30099
<i>Vireo altiloquus</i>	Macaulay	11704	0.546	2360	3842	21780
<i>Vireo osburni</i>	Macaulay	199938	1.44	2497	2756	5407
<i>Vireo solitarius</i>	Macaulay	219630	0.31	3092	4910	13824
<i>Vireo solitarius</i>	Macaulay	195784	0.28	3101	4453	18841
<i>Vireo solitarius</i>	Macaulay	133978	0.45	2627	4867	18755
<i>Vireo solitarius</i>	Macaulay	76517	0.29	2782	4221	15604
<i>Vireo solitarius</i>	Macaulay	11886	0.33	2326	4221	20735

<i>Vireo solitarius</i>	Macaulay	105404	0.29	2412	4996	19811
<i>Vireo solitarius</i>	Xeno-canto	XC389434	0.44	2485	4923	19456
<i>Vireo solitarius</i>	Xeno-canto	XC190933	0.42	2412	4358	35394
<i>Vireo solitarius</i>	Xeno-canto	XC188905	0.41	2898	5284	20689
<i>Vireo solitarius</i>	Xeno-canto	XC135497	0.3	2929	5685	19877
<i>Vireo leucophrys</i>	Macaulay	90078	1.486	2670	4324	18851
<i>Vireo leucophrys</i>	Xeno-canto	XC251742	1.683	2929	4737	23527
<i>Vireo leucophrys</i>	Xeno-canto	XC273783	1.974	2842	4307	15253
<i>Vireo leucophrys</i>	Xeno-canto	XC245586	1.788	3015	4871	16619
<i>Vireo leucophrys</i>	Xeno-canto	XC183705	1.254	2929	4823	16659
<i>Vireo leucophrys</i>	Xeno-canto	XC128052	1.463	2929	4479	15153
<i>Vireo leucophrys</i>	Xeno-canto	XC55136	2.775	2877	4737	16816
<i>Vireo leucophrys</i>	Xeno-canto	XC259171	1.823	2842	4651	16677
<i>Vireo leucophrys</i>	Xeno-canto	XC274268	1.277	3101	4651	17898
<i>Vireo leucophrys</i>	Xeno-canto	XC55136	2.774	2894	4737	15410

<i>Hylophilus</i>	Xeno-canto	XC201985	7.195	2756	3790	3161
<i>brunneiceps</i>						
<i>Hylophilus</i>	Xeno-canto	XC81004	19.795	2842	3531	2611
<i>brunneiceps</i>						
<i>Pachysylvia</i>	Xeno-canto	XC224373	0.58	2550	4755	30263
<i>muscapina</i>						
<i>Pachysylvia</i>	Xeno-canto	XC216489	0.6	2584	4819	18114
<i>muscapina</i>						
<i>Pachysylvia</i>	Xeno-canto	XC5397	0.66	2670	4419	20919
<i>muscapina</i>						
<i>Vireo cassinii</i>	Macaulay	192448	0.31	2808	4453	16482
<i>Vireo cassinii</i>	Macaulay	11919	0.44	2670	4414	13558
<i>Vireo cassinii</i>	Macaulay	105665	0.38	2894	4169	12181
<i>Vireo cassinii</i>	Macaulay	217624	0.29	3359	4462	15217
<i>Vireo cassinii</i>	Xeno-canto	XC189287	0.35	3015	4018	17432
<i>Vireo cassinii</i>	Xeno-canto	XC187484	0.3	2929	4608	15459

<i>Vireo cassinii</i>	Xeno-canto	XC135027	0.38	2231	4565	19859
<i>Vireo cassinii</i>	Xeno-canto	XC232107	0.35	2270	4221	24609
<i>Vireo cassinii</i>	Xeno-canto	XC128912	0.28	2929	5056	33198
<i>Vireo cassinii</i>	Xeno-canto	XC103095	0.35	2748	4009	19619
<i>Vireolanius melitophrys</i>	Macaulay	57726	0.848	2067	2911	7767
<i>Vireolanius melitophrys</i>	Macaulay	57704	0.859	1951	2959	6401
<i>Vireolanius melitophrys</i>	Xeno-canto	XC265104	0.755	2153	2825	6625
<i>Vireolanius melitophrys</i>	Xeno-canto	XC232220	0.673	1895	2929	8291
<i>Vireolanius melitophrys</i>	Xeno-canto	XC232218	0.918	1809	2584	6269
<i>Vireolanius melitophrys</i>	Xeno-canto	XC65616	0.696	1809	2502	7297

<i>Vireo chivi</i>	Macaulay	225001	0.267	2494	3971	13279
<i>Vireo chivi</i>	Macaulay	134256	0.267	2670	4100	19265
<i>Vireo chivi</i>	Macaulay	20040	0.279	2634	3704	31402
<i>Vireo chivi</i>	Macaulay	25331	0.348	2369	3755	17225
<i>Vireo chivi</i>	Macaulay	33817	0.395	2593	3661	11772
<i>Vireo chivi</i>	Macaulay	42888	0.418	2730	4393	18439
<i>Vireo chivi</i>	Macaulay	133276	0.244	3142	4656	38761
<i>Vireo chivi</i>	Macaulay	193170	0.325	2504	4716	33048
<i>Vireo chivi</i>	Macaulay	67081	0.313	2257	3745	25448
<i>Vireo chivi</i>	Macaulay	67086	0.244	2541	3704	17432
<i>Vireo bairdi</i>	Macaulay	103387	1.068	2498	4048	38019
<i>Vireo bairdi</i>	Xeno-canto	XC332423	1.196	2929	4556	26319
<i>Pachysylvia</i>	Macaulay	113099	0.685	2446	4134	12921
<i>hypoxantha</i>						
<i>Pachysylvia</i>	Macaulay	112876	0.685	2412	4134	15403
<i>hypoxantha</i>						

<i>Pachysylvia</i>	Macaulay	35513	0.754	2618	4186	17725
<i>hypoxantha</i>						
<i>Pachysylvia</i>	Xeno-canto	XC270733	0.696	2450	4143	17657
<i>hypoxantha</i>						
<i>Pachysylvia</i>	Xeno-canto	XC2836	0.662	2929	4221	16622
<i>hypoxantha</i>						
<i>Vireo nanus</i>	Xeno-canto	XC308600	1.219	2326	3187	16150
<i>Vireo nanus</i>	Xeno-canto	XC49010	1.149	2067	3101	19101
<i>Vireo nanus</i>	Xeno-canto	XC97161	1.115	2240	3015	22685
<i>Vireo nanus</i>	Macaulay	35343	1.474	2412	3187	14515
<i>Vireo nanus</i>	Macaulay	145654	1.208	2218	2670	12176
<i>Vireo hypochryseus</i>	Xeno-canto	XC378913	2.856	2498	3962	16570
<i>Vireo hypochryseus</i>	Xeno-canto	XC65646	1.51	2153	5263	19444
<i>Vireo hypochryseus</i>	Xeno-canto	XC330853	1.974	2498	4393	16417
<i>Vireo hypochryseus</i>	Xeno-canto	XC317984	2.345	2412	3811	20357
<i>Vireo hypochryseus</i>	Xeno-canto	XC232147	1.486	2670	3962	17857

<i>Vireo hypochryseus</i>	Xeno-canto	XC212642	2.066	2326	4221	22007
<i>Pachysylvia</i>	Xeno-canto	XC271334	0.91	2674	5599	28711
<i>aurantiifrons</i>						
<i>Pachysylvia</i>	Xeno-canto	XC143079	0.31	2593	4479	34016
<i>aurantiifrons</i>						
<i>Pachysylvia</i>	Xeno-canto	XC182280	0.44	2537	5190	30505
<i>aurantiifrons</i>						
<i>Pachysylvia</i>	Xeno-canto	XC224329	0.36	3049	5478	29454
<i>aurantiifrons</i>						
<i>Pachysylvia</i>	Macaulay	70354	0.36	2248	3867	28711
<i>aurantiifrons</i>						
<i>Pachysylvia</i>	Macaulay	70353	0.43	2756	5728	40520
<i>aurantiifrons</i>						
<i>Pachysylvia</i>	Macaulay	70345	0.34	3015	6365	24342
<i>aurantiifrons</i>						

<i>Pachysylvia</i>	Macaulay	10974	0.4	2670	5702	28464
<i>aurantiifrons</i>						
<i>Vireo vicinior</i>	Macaulay	56878	0.27	1731	3351	28711
<i>Vireo vicinior</i>	Macaulay	163241	0.3	1981	4083	14642
<i>Vireo vicinior</i>	Macaulay	105237	0.26	2158	3269	13377
<i>Vireo vicinior</i>	Macaulay	40629	0.21	2541	3445	20338
<i>Vireo vicinior</i>	Xeno-canto	XC282205	0.21	2472	3717	18742
<i>Vireo vicinior</i>	Xeno-canto	XC253192	0.15	2326	3549	16563
<i>Vireo vicinior</i>	Xeno-canto	XC205873	0.24	1637	3135	19738
<i>Vireo vicinior</i>	Xeno-canto	XC72274	0.17	2636	3730	19139
<i>Vireo vicinior</i>	Xeno-canto	XC161140	0.23	1873	3208	16149
<i>Vireo vicinior</i>	Xeno-canto	XC21665	0.21	2916	3902	12361
<i>Pteruthius</i>	Xeno-canto	XC299800	1.27	2756	4134	19878
<i>xanthochlorus</i>						
<i>Pteruthius</i>	Macaulay	180601	0.93	2584	3872	16786
<i>xanthochlorus</i>						

<i>Pteruthius</i>	Xeno-canto	XC256334	1	2606	4315	30864
<i>xanthochlorus</i>						
<i>Pteruthius</i>	Xeno-canto	XC69302	1.09	2929	4134	22771
<i>xanthochlorus</i>						
<i>Vireolanius</i>	Macaulay	527414	0.69	2153	2929	8156
<i>pulchellus</i>						
<i>Vireolanius</i>	Macaulay	165899	0.78	1981	3157	13159
<i>pulchellus</i>						
<i>Vireolanius</i>	Xeno-canto	XC309795	0.71	2326	3015	12920
<i>pulchellus</i>						
<i>Vireolanius</i>	Xeno-canto	XC199032	0.58	2412	2885	5557
<i>pulchellus</i>						
<i>Vireolanius</i>	Xeno-canto	XC31904	0.66	2326	2929	7177
<i>pulchellus</i>						
<i>Vireolanius</i>	Xeno-canto	XC271677	0.55	2240	2929	11858
<i>pulchellus</i>						

<i>Vireolanius</i>	Xeno-canto	XC232222	0.91	2326	3359	13996
<i>pulchellus</i>						
<i>Hylophilus</i>	Macaulay	109981	2.12	2584	3359	11189
<i>semicinereus</i>						
<i>Hylophilus</i>	Macaulay	219418	3.44	2842	3445	7670
<i>semicinereus</i>						
<i>Hylophilus</i>	Macaulay	52125	4.28	2584	3359	10729
<i>semicinereus</i>						
<i>Hylophilus</i>	Xeno-canto	XC38493	4.01	2240	3273	10951
<i>semicinereus</i>						
<i>Hylophilus</i>	Xeno-canto	XC327292	3.96	2326	3359	10287
<i>semicinereus</i>						
<i>Hylophilus</i>	Xeno-canto	XC211170	3.83	2240	3273	12116
<i>semicinereus</i>						
<i>Hylophilus</i>	Xeno-canto	XC139194	14.4	2584	3187	6964
<i>semicinereus</i>						

<i>Hylophilus</i>	Xeno-canto	XC122733	11.15	2412	3359	10407
<i>semicinereus</i>						
<i>Hylophilus</i>	Xeno-canto	XC59370	2.71	2842	3359	9323
<i>semicinereus</i>						
<i>Vireo huttoni</i>	Macaulay	192455	0.41	2653	5547	11093
<i>Vireo huttoni</i>	Macaulay	189350	0.3	2972	6697	26226
<i>Vireo huttoni</i>	Macaulay	109044	0.35	3178	5090	6700
<i>Vireo huttoni</i>	Macaulay	21400	0.45	2498	5797	16380
<i>Vireo huttoni</i>	Macaulay	163245	0.35	2188	5254	15593
<i>Vireo huttoni</i>	Macaulay	40617	0.41	2472	6451	31377
<i>Vireo huttoni</i>	Xeno-canto	XC232138	0.38	3187	6003	22065
<i>Vireo huttoni</i>	Xeno-canto	XC21395	0.3	3122	6159	20981
<i>Vireo huttoni</i>	Xeno-canto	XC30596	0.38	2808	5513	13920
<i>Vireo huttoni</i>	Xeno-canto	XC30596	0.38	2842	5754	11528
<i>Vireo modestus</i>	Macaulay	56135	0.84	1981	3131	14887
<i>Vireo modestus</i>	Xeno-canto	XC308426	1.21	2412	3402	30329

<i>Vireo modestus</i>	Xeno-canto	XC48134	1.01	3445	5340	33797
<i>Vireo modestus</i>	Xeno-canto	XC48130	0.89	3790	5969	35106
<i>Hylophilus</i> <i>thoracicus</i>	Xeno-canto	XC272367	2.345	2498	3531	16439
<i>Hylophilus</i> <i>thoracicus</i>	Xeno-canto	XC242050	2.415	2498	3187	6576
<i>Hylophilus</i> <i>thoracicus</i>	Xeno-canto	XC344752	2.182	2412	3015	8124
<i>Hylophilus</i> <i>thoracicus</i>	Xeno-canto	XC288198	2.938	2498	3704	12795
<i>Hylophilus</i> <i>thoracicus</i>	Xeno-canto	XC275114	1.904	2847	3790	12667
<i>Hylophilus</i> <i>thoracicus</i>	Xeno-canto	XC247220	2.357	2498	3359	8554
<i>Hylophilus</i> <i>thoracicus</i>	Xeno-canto	XC224440	1.857	2670	3531	8587

<i>Hylophilus</i>	Xeno-canto	XC224436	2.078	2791	3531	12241
<i>thoracicus</i>						
<i>Hylophilus</i>	Xeno-canto	XC391191	1.799	2636	3704	12966
<i>thoracicus</i>						
<i>Pachysylvia</i>	Xeno-canto	XC268528	0.52	3273	6473	25302
<i>decurtata</i>						
<i>Pachysylvia</i>	Xeno-canto	XC271337	0.34	3790	5857	31787
<i>decurtata</i>						
<i>Pachysylvia</i>	Xeno-canto	XC262345	0.55	3101	5099	17460
<i>decurtata</i>						
<i>Pachysylvia</i>	Xeno-canto	XC11098	0.38	3708	5534	24353
<i>decurtata</i>						
<i>Pachysylvia</i>	Xeno-canto	XC137711	0.55	3342	5461	17266
<i>decurtata</i>						
<i>Pachysylvia</i>	Xeno-canto	XC22488	0.5	2980	5340	18818
<i>decurtata</i>						

<i>Vireo pallens</i>	Xeno-canto	XC125976	1.44	2911	4479	22347
<i>Vireo pallens</i>	Xeno-canto	XC332788	1.52	2153	3101	14577
<i>Vireo pallens</i>	Xeno-canto	XC71800	1.58	2929	3876	16079
<i>Vireo pallens</i>	Xeno-canto	XC28469	1.38	3273	4466	14148
<i>Vireo pallens</i>	Xeno-canto	XC28469	2.26	2067	3445	33128
<i>Hylophilus olivaceus</i>	Xeno-canto	XC390646	1.47	2929	3531	7656
<i>Hylophilus olivaceus</i>	Xeno-canto	XC208693	3.03	3187	4134	7866
<i>Hylophilus olivaceus</i>	Xeno-canto	XC296708	3.5	3015	3962	8264
<i>Hylophilus olivaceus</i>	Xeno-canto	XC261029	2.91	3273	3962	8470
<i>Hylophilus olivaceus</i>	Xeno-canto	XC261028	3.69	2670	3618	11323
<i>Hylophilus olivaceus</i>	Xeno-canto	XC259177	2.55	2593	3618	17623
<i>Hylophilus olivaceus</i>	Xeno-canto	XC144645	1.96	2929	4479	10487
<i>Hylophilus olivaceus</i>	Xeno-canto	XC17380	2.72	3066	3962	9958
<i>Vireo latimeri</i>	Macaulay	129733	0.82	2326	4432	18082
<i>Vireo latimeri</i>	Xeno-canto	XC344045	0.71	2498	4625	17716
<i>Vireo latimeri</i>	Macaulay	129712	0.86	2097	4737	20337

<i>Vireo latimeri</i>	Xeno-canto	XC308505	0.69	2407	5004	20995
<i>Vireo latimeri</i>	Xeno-canto	XC33697	0.69	2175	4199	17632
<i>Vireo latimeri</i>	Xeno-canto	XC9424	0.57	2670	4651	18841
<i>Vireo philadelphicus</i>	Macaulay	11889	0.28	2343	4014	31519
<i>Vireo philadelphicus</i>	Macaulay	11887	0.57	2412	4492	25877
<i>Vireo philadelphicus</i>	Xeno-canto	XC22433	0.51	2584	5349	26600
<i>Vireo philadelphicus</i>	Xeno-canto	XC189443	0.29	2420	4208	20554
<i>Vireo philadelphicus</i>	Xeno-canto	XC55075	0.45	2373	3656	21758
<i>Vireo philadelphicus</i>	Xeno-canto	XC13584	0.34	2756	5254	28113
<i>Vireo philadelphicus</i>	Xeno-canto	XC189428	0.37	2696	4539	18343
<i>Vireo philadelphicus</i>	Macaulay	515858	0.44	2412	4134	28216
<i>Vireo philadelphicus</i>	Macaulay	188861	0.43	2420	4776	20187
<i>Vireo philadelphicus</i>	Macaulay	71229	0.38	2274	3790	21038
<i>Vireo plumbeus</i>	Macaulay	516714	0.27	2067	3962	27344
<i>Vireo plumbeus</i>	Macaulay	188811	0.41	2067	4074	12715
<i>Vireo plumbeus</i>	Macaulay	188323	0.36	2326	5642	18060

<i>Vireo plumbeus</i>	Macaulay	188265	0.33	2240	3704	17174
<i>Vireo plumbeus</i>	Macaulay	131237	0.58	1800	4048	18587
<i>Vireo plumbeus</i>	Macaulay	109026	0.38	2119	4048	20445
<i>Vireo plumbeus</i>	Macaulay	25178	0.28	2588	4044	21206
<i>Vireo plumbeus</i>	Macaulay	50222	0.3	1744	3488	17668
<i>Vireo plumbeus</i>	Xeno-canto	XC319004	0.29	2773	4737	28136
<i>Vireo plumbeus</i>	Xeno-canto	XC181494	0.22	2145	4255	21533
<i>Vireo olivaceus</i>	Macaulay	216854	0.67	2584	5767	42383
<i>Vireo olivaceus</i>	Macaulay	205374	0.74	2412	6115	30849
<i>Vireo olivaceus</i>	Macaulay	187059	0.3	2765	4823	25590
<i>Vireo olivaceus</i>	Macaulay	120457	0.33	2339	4354	26019
<i>Vireo olivaceus</i>	Macaulay	105271	0.27	2498	4307	25976
<i>Vireo olivaceus</i>	Macaulay	67814	0.33	2240	4109	30207
<i>Vireo olivaceus</i>	Macaulay	105485	0.35	2584	3833	19876
<i>Vireo olivaceus</i>	Macaulay	73959	0.28	2407	3811	29428
<i>Vireo olivaceus</i>	Macaulay	63933	0.56	2823	5612	16810

<i>Vireo olivaceus</i>	Macaulay	11867	0.41	2476	5426	29289
<i>Cyclarhis gujanensis</i>	Macaulay	134268	0.69	2240	3101	12303
<i>Cyclarhis gujanensis</i>	Macaulay	2139	0.94	2067	3359	10288
<i>Cyclarhis gujanensis</i>	Macaulay	129781	1.1	1723	2873	14938
<i>Cyclarhis gujanensis</i>	Xeno-canto	XC352263	1.45	1886	2842	13422
<i>Cyclarhis gujanensis</i>	Xeno-canto	XC329437	1.23	1981	3445	13144
<i>Cyclarhis gujanensis</i>	Macaulay	37750	0.98	1736	3015	11215
<i>Cyclarhis gujanensis</i>	Macaulay	28761	0.91	2412	3704	16634
<i>Cyclarhis gujanensis</i>	Macaulay	28245	0.86	1981	3320	15791
<i>Cyclarhis gujanensis</i>	Macaulay	20346	1.08	1550	2584	17061
<i>Cyclarhis gujanensis</i>	Macaulay	10964	1.08	1723	3183	11083
<i>Hylophilus poicilotis</i>	Macaulay	35734	1.38	2463	3704	16053
<i>Hylophilus poicilotis</i>	Macaulay	32062	1.83	3618	4483	15672
<i>Hylophilus poicilotis</i>	Macaulay	22121	1.2	3351	4320	19918
<i>Hylophilus poicilotis</i>	Macaulay	20142	1.42	3790	4974	20365
<i>Hylophilus poicilotis</i>	Macaulay	19838	1.66	3359	4737	16905

<i>Hylophilus poicilotis</i>	Xeno-canto	XC288584	1.88	3273	4737	19851
<i>Hylophilus poicilotis</i>	Xeno-canto	XC211117	2.14	3618	4944	14872
<i>Hylophilus poicilotis</i>	Xeno-canto	XC60490	1.18	3618	5392	21111
<i>Pachysylvia</i>	Xeno-canto	XC273433	1.01	2929	4462	16895
<i>semibrunnea</i>						
<i>Pachysylvia</i>	Xeno-canto	XC82603	0.78	2670	4134	15381
<i>semibrunnea</i>						
<i>Pachysylvia</i>	Xeno-canto	XC157663	0.53	2972	4134	14587
<i>semibrunnea</i>						
<i>Pachysylvia</i>	Xeno-canto	XC130753	0.65	3015	3962	17326
<i>semibrunnea</i>						
<i>Hylophilus flavipes</i>	Macaulay	70322	4.08	2929	3876	13604
<i>Hylophilus flavipes</i>	Macaulay	10992	4.1	2584	3962	18565
<i>Hylophilus flavipes</i>	Macaulay	70331	3.24	2670	3962	14772
<i>Hylophilus flavipes</i>	Macaulay	70328	4.9	2756	4048	12691
<i>Hylophilus flavipes</i>	Macaulay	70324	2.89	2756	4048	14894

<i>Hylophilus flavipes</i>	Xeno-canto	XC354334	3.16	3015	3876	14015
<i>Hylophilus flavipes</i>	Xeno-canto	XC273728	4.54	2929	3962	19677
<i>Hylophilus flavipes</i>	Xeno-canto	XC273526	3.25	3015	4048	20400
<i>Hylophilus flavipes</i>	Xeno-canto	XC16065	2.62	2756	3359	6031
<i>Vireo brevipennis</i>	Macaulay	136555	0.87	2205	5409	26281
<i>Vireo brevipennis</i>	Macaulay	57712	0.73	2373	5935	21810
<i>Vireo brevipennis</i>	Macaulay	56627	0.87	1977	5090	27753
<i>Vireo brevipennis</i>	Xeno-canto	XC254070	0.94	2093	4996	23354
<i>Vireo brevipennis</i>	Xeno-canto	XC190546	0.98	1809	4750	21781
<i>Vireo brevipennis</i>	Xeno-canto	XC319501	0.73	1951	3734	21671
<i>Vireo brevipennis</i>	Xeno-canto	XC232105	0.95	1981	4664	25121
<i>Vireolanius leucotis</i>	Macaulay	114963	0.56	1667	2670	2093
<i>Vireolanius leucotis</i>	Macaulay	72490	0.66	1763	2601	1763
<i>Vireolanius leucotis</i>	Xeno-canto	XC272163	0.6	1981	2364	828
<i>Vireolanius leucotis</i>	Xeno-canto	XC232206	0.57	1895	2636	1611
<i>Vireolanius leucotis</i>	Xeno-canto	XC148261	0.64	2326	2584	1436

<i>Vireolanius leucotis</i>	Xeno-canto	XC148261	0.48	1981	2416	1077
<i>Vireolanius leucotis</i>	Xeno-canto	XC232202	0.6	2067	2364	828
<i>Vireolanius leucotis</i>	Xeno-canto	XC27834	0.45	1981	2507	1657
<i>Tunchiornis</i> <i>ochraceiceps</i>	Xeno-canto	XC388512	0.69	2756	2842	122
<i>Tunchiornis</i> <i>ochraceiceps</i>	Xeno-canto	XC309788	0.41	2929	3531	1689
<i>Tunchiornis</i> <i>ochraceiceps</i>	Xeno-canto	XC270735	0.88	2756	3045	776
<i>Tunchiornis</i> <i>ochraceiceps</i>	Xeno-canto	XC203229	0.75	2929	3618	1009
<i>Tunchiornis</i> <i>ochraceiceps</i>	Xeno-canto	XC94781	0.87	3015	3273	1340
<i>Tunchiornis</i> <i>ochraceiceps</i>	Xeno-canto	XC81854	0.73	2670	2929	342

<i>Tunchiornis</i>	Macaulay	527264	0.66	3618	3704	422
<i>ochraceiceps</i>						
<i>Vireo sclateri</i>	Xeno-canto	XC1172	0.88	2842	4221	3121
<i>Greenlet</i>						
<i>Vireo sclateri</i>	Xeno-canto	XC224424	1.01	2929	4432	3788
<i>Greenlet</i>						
<i>Vireo crassirostris</i>	Xeno-canto	XC331618	1.29	1637	5943	25531
<i>Vireo crassirostris</i>	Xeno-canto	XC140233	1.61	1878	6253	24567
<i>Vireo crassirostris</i>	Xeno-canto	XC28588	1.47	2033	5581	27531
<i>Vireo crassirostris</i>	Xeno-canto	11737	0.94	2067	5680	32150
<i>Vireo crassirostris</i>	Xeno-canto	XC105959	1.23	1895	5254	26019
<i>Vireo crassirostris</i>	Xeno-canto	XC331617	1.21	1809	4182	22542
<i>Vireo crassirostris</i>	Xeno-canto	XC146590	1.09	1550	5155	32747
<i>Vireo gilvus</i>	Macaulay	222051	1.44	2498	4543	22200
<i>Vireo gilvus</i>	Macaulay	195761	2.36	2498	4823	18979
<i>Vireo gilvus</i>	Macaulay	172246	1.74	2972	5082	26965

<i>Vireo gilvus</i>	Macaulay	144024	1.8	2412	5392	30557
<i>Vireo gilvus</i>	Macaulay	45187	1.61	2623	5426	21663
<i>Vireo gilvus</i>	Macaulay	105644	3.32	2498	4307	16089
<i>Vireo gilvus</i>	Xeno-canto	XC378147	3.5	2584	4651	22363
<i>Vireo gilvus</i>	Xeno-canto	XC324999	2.35	2412	5168	29186
<i>Vireo gilvus</i>	Xeno-canto	XC188163	2.37	2498	5375	27453
<i>Vireo gilvus</i>	Xeno-canto	XC195842	1.71	2700	4363	23736
<i>Erpornis zantholeuca</i>	Macaulay	76919	0.662	5254	6718	16282
<i>Vireo griseus</i>	Macaulay	534380	0.99	1981	5513	30196
<i>Vireo griseus</i>	Macaulay	135398	1.03	1809	4660	24561
<i>Vireo griseus</i>	Macaulay	105227	1.24	2028	5034	28911
<i>Vireo griseus</i>	Macaulay	100799	1.05	1990	4729	27799
<i>Vireo griseus</i>	Macaulay	94316	0.91	2140	6301	26854
<i>Vireo griseus</i>	Macaulay	XC381101	1.44	2326	5185	35645
<i>Vireo griseus</i>	Xeno-canto	XC53793	0.86	2024	3661	17874
<i>Vireo griseus</i>	Xeno-canto	XC33625	1.2	1809	5426	60952

<i>Vireo griseus</i>	Xeno-canto	XC21959	0.92	2067	4651	26917
<i>Vireo griseus</i>	Xeno-canto	XC309815	1.09	2804	4432	16012
<i>Vireolanius eximius</i>	Macaulay	67092	0.96	2153	2584	4950
<i>Vireolanius eximius</i>	Xeno-canto	XC353908	0.8	2115	2584	2307
<i>Vireolanius eximius</i>	Xeno-canto	XC273597	0.79	2123	2584	4785
<i>Vireo flavoviridis</i>	Macaulay	20384	0.21	3247	5267	45458
<i>Vireo flavoviridis</i>	Macaulay	89524	0.14	2438	4040	32899
<i>Vireo flavoviridis</i>	Xeno-canto	XC378078	0.19	2929	4160	22012
<i>Vireo flavoviridis</i>	Xeno-canto	XC366646	0.17	3066	4358	21533
<i>Vireo flavoviridis</i>	Xeno-canto	XC332952	0.16	2640	4970	37426
<i>Vireo flavoviridis</i>	Xeno-canto	XC252426	0.09	5233	6718	28713
<i>Vireo flavoviridis</i>	Xeno-canto	XC28547	0.13	2756	5082	46329
<i>Vireo flavoviridis</i>	Xeno-canto	XC232110	0.13	2627	3876	21533
<i>Vireo flavoviridis</i>	Xeno-canto	XC232110	0.21	2842	4737	15552
<i>Vireo flavoviridis</i>	Xeno-canto	XC77748	0.15	3239	4772	24294
<i>Vireo flavifrons</i>	Macaulay	220746	0.44	2041	3704	14922

<i>Vireo flavifrons</i>	Macaulay	110258	0.3	3101	3898	20704
<i>Vireo flavifrons</i>	Macaulay	105426	0.4	2412	3562	6966
<i>Vireo flavifrons</i>	Macaulay	105242	0.33	2873	4104	10510
<i>Vireo flavifrons</i>	Macaulay	79436	0.36	2110	3747	9494
<i>Vireo flavifrons</i>	Macaulay	73971	0.34	2584	4100	11137
<i>Vireo flavifrons</i>	Xeno-canto	XC325519	0.38	2067	3221	12180
<i>Vireo flavifrons</i>	Xeno-canto	XC100599	0.35	2192	3510	12441
<i>Vireo flavifrons</i>	Xeno-canto	XC100599	0.31	2179	3876	9836
<i>Vireo flavifrons</i>	Xeno-canto	XC177383	0.33	2730	3760	10510
<i>Vireo carmioli</i>	Xeno-canto	XC72470	0.627	2946	6202	31582
<i>Vireo carmioli</i>	Xeno-canto	XC97453	0.337	3187	5495	29336
<i>Vireo carmioli</i>	Xeno-canto	XC65669	0.162	4436	5986	24795
<i>Vireo carmioli</i>	Xeno-canto	XC52421	0.29	3032	6718	27849
<i>Vireo carmioli</i>	Xeno-canto	XC271674	0.615	3088	7235	36834
<i>Vireo carmioli</i>	Xeno-canto	XC107557	0.255	3730	5538	24556
<i>Vireo carmioli</i>	Macaulay	165870	0.383	2455	5211	24081

<i>Vireo carmioli</i>	Macaulay	37754	0.278	2670	5426	34864
<i>Vireo carmioli</i>	Xeno-canto	XC7843	0.174	3704	4565	21533
<i>Vireo magister</i>	Xeno-canto	XC369834	0.57	2416	5758	20880
<i>Vireo magister</i>	Xeno-canto	XC332412	0.21	2412	4014	14356
<i>Vireo magister</i>	Xeno-canto	XC355877	0.33	2153	3101	18115
<i>Vireo magister</i>	Xeno-canto	XC40535	0.12	2450	4699	27276
<i>Vireo magister</i>	Xeno-canto	XC353716	0.41	2007	4203	19035

Table 2.S3. Summary of results from phylogenetic principal components analysis using six measures of the bills of Vireonidae and my MCC Vireonidae tree. The percent of variance was calculated by dividing each axes' eigenvalue by the summed eigenvalues.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
LBN	0.56	0.31	-0.26	0.26	-0.29	-0.61
LEC	0.51	0.40	-0.30	-0.08	0.20	0.67
WBB	0.36	0.18	0.70	-0.54	0.13	-0.18
DBN	0.35	-0.58	-0.02	-0.22	-0.66	0.25
DBB	0.32	-0.58	-0.29	-0.12	0.64	-0.23
WBN	0.28	-0.20	0.51	0.75	0.12	0.19
Percent of variance	72.5	16.7	5.6	3.8	0.7	0.6

LBN: length of bill from the anterior margin of the naris to the tip; LEC: length of exposed culmen; WBB: width of bill at its base; DBN: depth of bill at the anterior margin of the naris; DBB: depth of bill at its base; WBN: width of bill at the anterior margin of the naris.

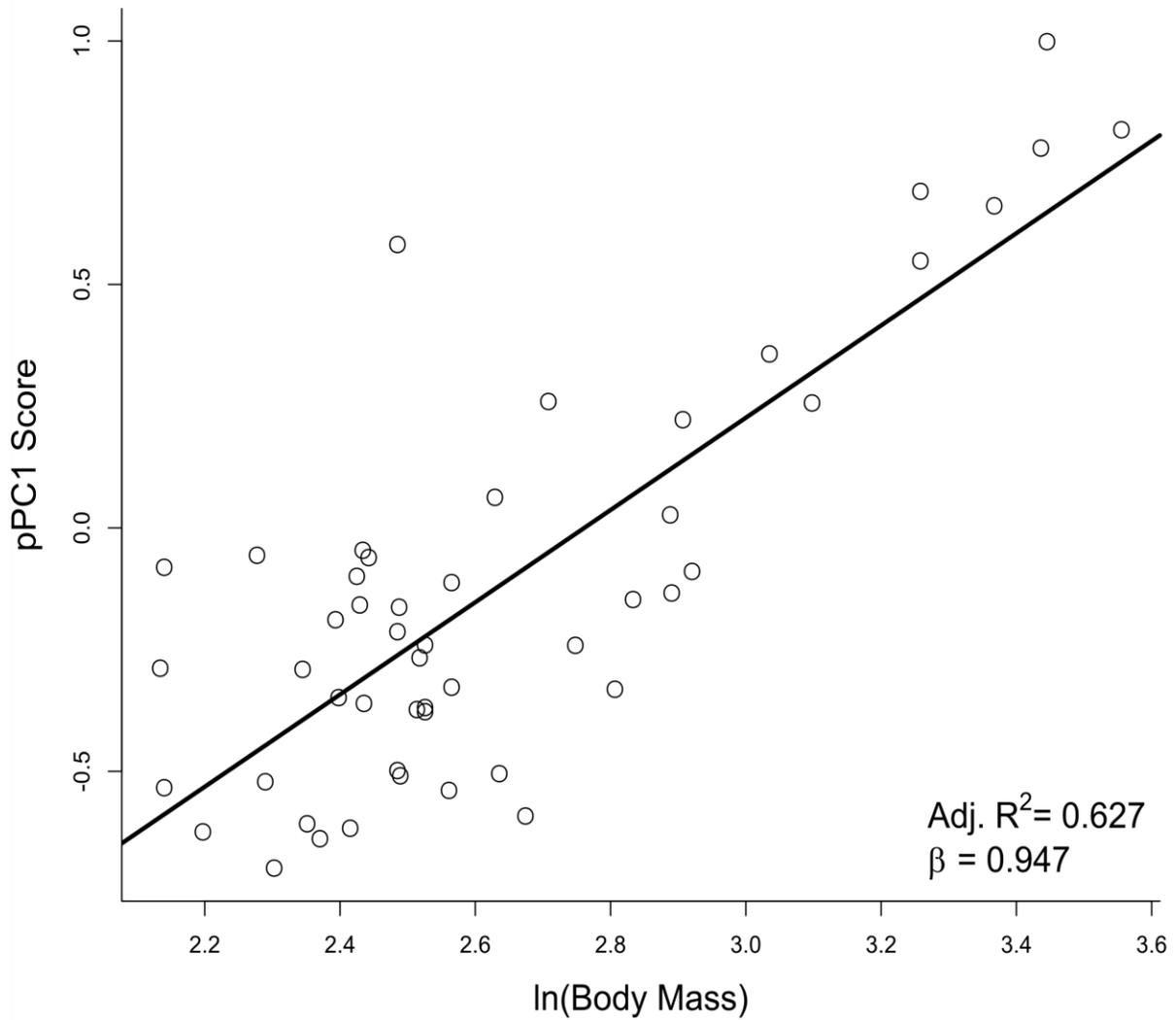


Figure 2.S2. Relationship between pPC1 and body mass (ln). pPC1 scores are largely predicted by a species' body mass. The slope of this relationship, noted by the black regression line, is highly significant and nearly equal to 1.0.

Table 3.S1. Song measurements from 137 individuals from 38 species of male vireonids. Songs were collected from Macaulay (ML) and Xeno-canto (XC) libraries; songs from *V. griseus bermudianus* were recorded in the field by me for this study. I viewed each recording as a waveform and spectrogram (Hamming window, FFT size = 512 samples, 87.5% overlap) using Raven Pro v1.5 sound analysis software (Charif et al., 2010).

Species	Recording ID	Song Length (s)	Minimum Peak Frequency (Hz)	Frequency Modulation (Hz/s)
<i>H. pectoralis</i>	XC-224406	1.28	2799.30	7965.24
<i>H. pectoralis</i>	ML-51872	1.40	2627.10	8064.14
<i>V. bellii</i>	ML-212118	0.98	2624.90	22789.97
<i>V. bellii</i>	ML-188220	1.34	2584.00	26658.24
<i>V. bellii</i>	ML-56857	1.16	2950.00	28059.85
<i>V. griseus bermudianus</i>	GreenYellow	0.92	1993.98	25007.37
<i>V. griseus bermudianus</i>	Orange	0.74	2058.60	14761.30
<i>V. griseus bermudianus</i>	BlueWhiteBlue	1.25	1938.00	31480.47
<i>V. griseus bermudianus</i>	UnknownVireo	1.48	2046.76	25277.73
<i>V. griseus bermudianus</i>	BlueOrange	0.93	2153.35	26866.21
<i>V. griseus bermudianus</i>	Yellow	1.00	1981.10	30029.06
<i>V. griseus bermudianus</i>	Red	0.79	2436.50	20422.58
<i>V. griseus bermudianus</i>	BlueRedWhite	0.91	2201.78	26971.66
<i>V. griseus bermudianus</i>	GreenRed	1.03	2207.18	32068.59
<i>V. griseus bermudianus</i>	RedWhiteBlue	1.00	2113.48	20383.84
<i>C. nigrostris</i>	XC-222154	1.32	1938.00	10264.34
<i>C. nigrostris</i>	XC-22416	1.07	1593.50	11125.12
<i>C. nigrostris</i>	XC-347862	0.87	2368.70	5197.70

<i>C. nigirostris</i>	XC-386840	0.88	1851.90	7725.14
<i>C. nigirostris</i>	XC-252845	0.88	2153.30	7763.61
<i>C. nigirostris</i>	XC-57389	0.86	2110.30	6459.83
<i>C. nigirostris</i>	XC-386721	0.86	2067.20	6211.54
<i>C. nigirostris</i>	XC-128606	1.31	1765.70	7633.20
<i>V. atricapilla</i>	XC-160976	0.45	3080.31	39452.08
<i>V. atricapilla</i>	XC-34845	0.97	3039.41	40057.80
<i>V. atricapilla</i>	ML-188204	0.84	2885.45	21300.12
<i>V. atricapilla</i>	XC-21738	0.51	2649.67	27894.76
<i>Pt. rufiventer</i>	ML-221817	0.41	1838.98	7803.54
<i>Pt. rufiventer</i>	ML-53562	0.62	1894.93	7226.46
<i>Pt. rufiventer</i>	ML-175231	0.40	1823.84	7520.48
<i>V. altiloquus</i>	ML-105336	0.66	2267.45	20278.25
<i>V. altiloquus</i>	ML-135938	0.63	2155.51	24351.10
<i>V. altiloquus</i>	ML-38464	0.62	2239.50	26417.69
<i>V. solitarius</i>	XC-135497	0.40	2909.12	16764.35
<i>V. solitarius</i>	XC-389434	0.39	2598.01	18683.30
<i>V. leucophrys</i>	XC-245586	1.22	3014.60	16564.82
<i>V. leucophrys</i>	XC-274268	1.42	3186.90	22175.65
<i>V. leucophrys</i>	XC-183705	1.36	2950.05	20677.71
<i>V. cassinii</i>	ML-105665	0.43	2557.08	17588.51
<i>Vl. melitophrys</i>	XC-232218	0.92	1808.80	6678.27
<i>Vl. melitophrys</i>	XC-265104	0.75	2153.30	6151.72
<i>Vl. melitophrys</i>	XC-65616	0.72	1851.90	7582.80
<i>Vl. melitophrys</i>	XC-232220	0.68	1851.90	7299.15
<i>V. chivi</i>	ML-225001	0.32	2590.45	16766.64
<i>V. chivi</i>	ML-134256	0.26	2601.20	19743.88
<i>P. hypoxantha</i>	ML-113099	0.70	2774.57	19324.09

<i>P. hypoxantha</i>	XC-270733	0.68	2595.83	24993.28
<i>V. nanus</i>	ML-145654	1.30	2196.40	12832.70
<i>V. nanus</i>	XC-97161	1.13	2239.50	21957.91
<i>V. nanus</i>	ML-35343	1.47	2411.70	14278.81
<i>V. nanus</i>	XC-49010	1.15	2110.30	18767.49
<i>V. nanus</i>	XC-308600	1.22	2366.55	16029.44
<i>P. aurantiifrons</i>	ML-70354	0.35	2550.62	24192.92
<i>P. aurantiifrons</i>	ML-70345	0.40	2871.43	27878.98
<i>P. aurantiifrons</i>	XC-143079	0.31	2786.43	37326.85
<i>P. aurantiifrons</i>	ML-70353	0.41	3074.93	33275.54
<i>P. aurantiifrons</i>	XC-224329	0.35	3071.70	26598.24
<i>V. vicinior</i>	ML-56878	0.23	1975.69	22141.84
<i>V. vicinior</i>	XC-72274	0.18	2282.55	14460.23
<i>V. vicinior</i>	ML-40629	0.24	1549.32	20285.30
<i>Pt. xanthochlorus</i>	ML-180601	0.91	2648.60	15780.01
<i>Pt. xanthochlorus</i>	XC-69302	1.20	2788.55	18179.33
<i>Vl. pulchellus</i>	ML-527414	0.67	2157.61	9013.76
<i>Vl. pulchellus</i>	XC-199032	0.58	2368.70	5981.06
<i>Vl. pulchellus</i>	XC-271677	0.57	2211.49	10894.05
<i>Vl. pulchellus</i>	XC-232222	0.87	2540.90	11663.99
<i>Vl. pulchellus</i>	XC-31904	0.65	2325.60	9569.68
<i>H. semicinereus</i>	XC-59370	2.77	2758.36	9711.11
<i>H. semicinereus</i>	XC-38493	3.98	2338.52	10889.57
<i>V. huttoni</i>	ML-109044	0.39	3219.19	9506.00
<i>H. thoracicus</i>	XC-272367	2.21	2540.90	15274.13
<i>H. thoracicus</i>	XC-224436	2.05	2799.30	12512.09
<i>H. thoracicus</i>	XC-391191	1.54	2670.10	13929.82
<i>P. decurtata</i>	XC-11098	0.34	3529.28	26416.44

<i>P. decurtata</i>	XC-137711	0.46	3675.69	22833.96
<i>P. decurtata</i>	XC-262345	0.49	3264.40	17102.94
<i>V. griseus</i>	ML-100799	1.07	2269.62	29071.71
<i>V. griseus</i>	XC-33625	0.93	2196.40	35230.01
<i>V. philadelphicus</i>	ML-515858	0.41	2398.80	25557.56
<i>V. philadelphicus</i>	XC-22433	0.44	2571.07	29910.31
<i>V. philadelphicus</i>	ML-71229	0.28	2705.66	17405.86
<i>V. philadelphicus</i>	ML-188861	0.41	2478.48	22999.22
<i>V. philadelphicus</i>	XC-13584	0.31	2757.33	25366.86
<i>V. philadelphicus</i>	XC-189428	0.39	2702.43	18349.37
<i>V. philadelphicus</i>	XC-189443	0.33	2611.96	32233.73
<i>V. philadelphicus</i>	ML-11889	0.24	2553.83	30622.27
<i>V. plumbeus</i>	ML-50222	0.30	1963.85	21341.24
<i>V. plumbeus</i>	XC-181494	0.27	2131.80	27346.99
<i>V. plumbeus</i>	ML-131237	0.30	2492.50	27744.07
<i>V. plumbeus</i>	XC-319004	0.28	2380.50	18729.95
<i>V. olivaceus</i>	ML-67814	0.51	2304.05	26006.58
<i>V. olivaceus</i>	ML-105485	0.31	2784.26	32689.67
<i>V. olivaceus</i>	ML-216854	0.39	2407.41	22982.22
<i>V. olivaceus</i>	ML-187059	0.27	2609.81	22511.93
<i>V. olivaceus</i>	ML-73959	0.27	2411.75	30415.00
<i>C. gujanensis</i>	XC-329437	1.23	2054.29	10305.98
<i>C. gujanensis</i>	XC-352263	1.46	1808.80	13786.72
<i>C. gujanensis</i>	ML-129781	1.10	1722.70	15790.56
<i>C. gujanensis</i>	ML-10964	1.06	1907.87	11231.33
<i>C. gujanensis</i>	ML-134268	0.68	2239.50	11438.72
<i>C. gujanensis</i>	ML-2139	0.91	2067.20	10374.55
<i>H. poicilotis</i>	XC211117	2.10	3574.50	13842.68

<i>H. poicilotis</i>	ML-20142	1.36	3781.20	20647.51
<i>H. poicilotis</i>	ML-32062	1.71	3561.57	16446.67
<i>H. flavipes</i>	XC16065	2.29	2756.20	5874.95
<i>H. flavipes</i>	ML-10992	4.10	2584.00	18514.89
<i>H. flavipes</i>	XC273526	3.27	2997.40	20712.31
<i>H. flavipes</i>	ML-70331	3.20	2713.20	15305.77
<i>H. flavipes</i>	ML-70324	2.87	3014.60	11648.30
<i>V. brevipennis</i>	ML-56627	0.82	2131.80	26328.82
<i>V. brevipennis</i>	ML-136555	0.68	2229.76	27915.00
<i>V. brevipennis</i>	XC190546	0.93	2055.35	25387.40
<i>Vl. leucotis</i>	XC-232206	0.53	1948.78	1716.49
<i>Vl. leucotis</i>	XC-261021	0.51	1981.10	1251.94
<i>Vl. leucotis</i>	XC-148261	0.65	2325.60	1793.15
<i>T. orhraceiceps</i>	XC-203229	0.74	2928.50	1562.77
<i>T. orhraceiceps</i>	XC-81854	0.72	2713.20	1042.47
<i>T. orhraceiceps</i>	ML-527264	0.64	3574.50	609.75
<i>T. orhraceiceps</i>	XC-388512	0.53	2756.20	234.24
<i>V. crassirostris</i>	XC-105959	1.30	2058.62	27878.59
<i>V. crassirostris</i>	ML-11737	1.11	2108.13	47498.69
<i>V. gilvus</i>	ML-195761	2.20	2390.20	17044.92
<i>V. gilvus</i>	ML-105644	2.94	2476.35	14687.37
<i>V. gilvus</i>	XC-324999	2.95	2562.45	24578.56
<i>V. gilvus</i>	ML-144024	1.50	2691.65	25069.48
<i>Vl. eximius</i>	ML-67092	0.95	2153.30	5012.36
<i>Vl. eximius</i>	XC-353908	0.81	2110.30	4785.38
<i>Vl. eximius</i>	XC-273597	0.79	2110.30	4502.27
<i>V. flavoviridis</i>	XC-378078	0.15	2753.02	16704.62
<i>V. flavoviridis</i>	XC-252426	0.14	4331.38	26916.44

<i>V. flavoviridis</i>	XC-232110	0.12	3273.05	29833.71
<i>V. flavifrons</i>	ML-73971	0.35	2410.65	12447.19
<i>V. flavifrons</i>	ML-110258	0.38	2556.00	13005.28
<i>V. carmioli</i>	XC-7843	0.27	3100.80	20916.78
<i>V. carmioli</i>	ML-37754	0.21	3152.47	30788.24
<i>V. magister</i>	XC-353716	0.39	1997.20	16760.62
<i>V. magister</i>	XC-40535	0.28	1869.09	22929.45

Although species with fewer than 2 recordings were excluded from my analyses, we still included *V. huttoni* and *V. cassini* in our table, despite having only 1 recording each. This is because these two species had two or more recordings available, but were only randomly selected once for use during the playback experiment.

Table 3.S2. Song structure of 38 vireonid species and Bermuda Vireo subspecies used as stimuli in 165 playback trials to 15 male Bermuda Vireos. Also shown are the phylogenetic distances between each species and Bermuda Vireo.

Species	Song duration (s)	Min Peak Freq (Hz)	Freq Mod (Hz/s)	Phylogenetic Distance (substitutions/site)
<i>Pt. xanthochlorus</i> (2)	1.06 ± 0.21	2719 ± 99	16980 ± 1697	30.51
<i>Pt. rufiventer</i> (3)	0.48 ± 0.12	1853 ± 37	7517 ± 289	30.51
<i>Vl. melitophrys</i> (4)	0.77 ± 0.11	1916 ± 159	6928 ± 641	20.86
<i>Vl. pulchellus</i> (5)	0.67 ± 0.12	2321 ± 149	9425 ± 2192	20.86
<i>Vl. leucotis</i> (3)	0.56 ± 0.08	2085 ± 209	1587 ± 293	20.86
<i>Vl. eximius</i> (3)	0.85 ± 0.09	2125 ± 25	4767 ± 256	20.86
<i>H. poicilotis</i> (3)	1.72 ± 0.37	3639 ± 123	16979 ± 3433	19.57
<i>H. pectoralis</i> (2)	1.34 ± 0.08	2713 ± 122	8015 ± 70	19.57
<i>H. semicinereus</i> (2)	3.38 ± 0.86	2548 ± 297	10300 ± 833	19.57
<i>H. flavipes</i> (5)	3.15 ± 0.66	2813 ± 187	14411 ± 5870	19.57
<i>H. thoracicus</i> (3)	1.93 ± 0.35	2670 ± 129	13905 ± 1381	19.57
<i>T. orhraceiceps</i> (4)	0.66 ± 0.10	2993 ± 399	862 ± 572	15.81
<i>V. vicinior</i> (3)	0.22 ± 0.03	1936 ± 368	18962 ± 4008	11.42
<i>V. huttoni</i> (1)	0.39	3219	9506	11.42
<i>V. flavifrons</i> (2)	0.37 ± 0.02	2483 ± 103	12726 ± 395	11.42
<i>V. solitarius</i> (2)	0.40 ± 0.01	2754 ± 220	17724 ± 1357	11.42
<i>V. plumbeus</i> (4)	0.29 ± 0.02	2242 ± 239	23791 ± 4468	11.42
<i>V. cassinii</i> (1)	0.43	2557	17589	11.42

<i>V. carmioli</i> (2)	0.24 ± 0.04	3127 ± 37	25853 ± 6980	11.42
<i>V. nanus</i> (5)	1.25 ± 0.14	2265 ± 124	16773 ± 3646	8.74
<i>V. griseus bermudianus</i> (10)	1.01 ± 0.22	2113 ± 146	25327 ± 5485	0.00
<i>V. griseus</i> (2)	1.00 ± 0.10	2233 ± 52	32151 ± 4355	0.06
<i>V. crassirostris</i> (2)	1.21 ± 0.13	2083 ± 35	37689 ± 13874	0.57
<i>V. bellii</i> (3)	1.16 ± 0.18	2720 ± 201	25836 ± 2729	8.07
<i>V. brevipennis</i> (3)	0.81 ± 0.13	2139 ± 87	26544 ± 1277	8.07
<i>V. atricapilla</i> (4)	0.69 ± 0.25	2914 ± 195	32176 ± 9159	8.07
<i>V. flavoviridis</i> (3)	0.14 ± 0.02	3452 ± 804	24485 ± 6894	14.10
<i>V. olivaceus</i> (5)	0.35 ± 0.10	2503 ± 192	26921 ± 4508	14.10
<i>V. magister</i> (2)	0.34 ± 0.08	1933 ± 91	19845 ± 4362	14.10
<i>V. chivi</i> (2)	0.29 ± 0.04	2596 ± 8	18255 ± 2105	14.10
<i>V. altiloquus</i> (3)	0.64 ± 0.02	2221 ± 58	23682 ± 3124	14.10
<i>V. philadelphicus</i> (8)	0.35 ± 0.07	2597 ± 122	25306 ± 5525	14.10
<i>V. leucophrys</i> (3)	1.33 ± 0.10	3051 ± 122	19806 ± 2905	14.10
<i>V. gilvus</i> (4)	2.40 ± 0.69	2530 ± 129	20345 ± 5264	14.10
<i>P. decurtata</i> (3)	0.43 ± 0.08	3490 ± 208	22118 ± 4698	14.60
<i>P. hypoxantha</i> (2)	0.69 ± 0.01	2685 ± 126	22159 ± 4009	14.60
<i>P. aurantiifrons</i> (5)	0.36 ± 0.04	2871 ± 219	29855 ± 5341	14.60
<i>C. nigrostris</i> (8)	1.01 ± 0.20	1981 ± 245	7798 ± 2009	21.71
<i>C. gujanensis</i> (6)	1.07 ± 0.27	1967 ± 190	12155 ± 2183	21.71

Details of song recording sampling, vireonid singing styles, and phylogenetic analyses are provided in the methods. Vireonids are ordered as they appear on the maximum clade credibility Vireonidae tree (Fig. 3.2). Numbers next to scientific names represent the number of individual playback sequences constructed for use across playback trials, per species. Values are mean ± SD and

are based on all playback sequences used during playbacks; sequences that were used more than once were only used once in above calculations. For sequences containing two song types, the average measurements of the two song types were used here. Although species with fewer than 2 recordings were excluded from my analyses, we still included *V. huttoni* and *V. cassini* in our table, despite having only 1 recording each. This is because these two species had two or more recordings available, but each species was only randomly selected once for use during the playback experiment.

Table 3.S3. Relationships between the strength of response of 15 male Bermuda Vireos to playbacks and the phylogenetic distance between Bermuda Vireos and the playback stimulus species. Model results for trial order are also presented. Trials involving consubspecific stimuli have been excluded ($N = 15$). Statistically significant P -values, relative to an adjusted alpha of 0.0167, are in bold. All variance inflation factors (VIFs) were < 5 , indicating low collinearity among model predictor variables.

Model	Factor	Coefficient (\pm SE)	Test stat	P	VIF
Total	Intercept	3.67 ± 0.47	7.8	< 0.0001	
vocalizations (GLMM)	Phylogenetic distance	-0.02 ± 0.02	-1.5	0.125	1.20
	Trial number	-0.14 ± 0.05	-3.0	0.002	1.20
Flyovers (GLMM)	Intercept	-0.14 ± 1.01	-0.1	0.892	
	Phylogenetic distance	-0.15 ± 0.03	-5.7	< 0.0001	1.02
	Trial number	-0.24 ± 0.08	-3.1	0.0017	1.02
Closest approach (LMM)	Intercept	1.78 ± 0.55	3.2	0.0015	
	Phylogenetic distance	0.08 ± 0.02	3.6	0.0005	1.03
	Trial number	0.21 ± 0.05	4.0	0.0001	1.03

$n = 150$ trials distributed evenly among 15 subjects. Random effects (variance \pm SD) for total vocalizations: 0.14 ± 0.38 ; flyovers: 3.49 ± 1.87 ; closest approach: 0.42 ± 0.65 , residual = 3.94 ± 1.99 . Test statistic for generalized linear mixed model (GLMM) was z ; test statistic for linear mixed model (LMM) was t .

Table 3.S4. Relationships between the strength of response of 15 male Bermuda Vireos to playbacks and the acoustic distance between Bermuda Vireos and the playback species. Model results for trial order are also presented. Trials involving consubspecific stimuli have been excluded ($N = 15$). Statistically significant P -values, relative to an adjusted alpha of 0.0167, are in bold. All variance inflation factors (VIFs) were < 5 , indicating low collinearity among model predictor variables.

Model	Factor	Coefficient (\pm SE)	Test stat	P	VIF
Total	Intercept	4.04 \pm 0.46	8.7	< 0.0001	
vocalizations (GLMM)	Acoustic distance	-2.20 \pm 0.83	-2.7	0.0082	1.10
	Trial number	-0.14 \pm 0.04	-3.3	0.001	1.10
Flyovers (GLMM)	Intercept	0.09 \pm 1.10	0.1	0.937	
	Acoustic distance	-7.74 \pm 1.65	-4.7	< 0.0001	1.01
	Trial number	-0.24 \pm 0.07	-3.5	0.0005	1.01
Closest approach (LMM)	Intercept	2.48 \pm 0.60	4.2	< 0.0001	
	Acoustic distance	1.68 \pm 1.10	1.5	0.127	1.03
	Trial number	0.19 \pm 0.05	3.5	0.0007	1.03

$n = 150$ trials distributed evenly among 15 subjects. Random effects (variance \pm SD) for total vocalizations: 0.16 \pm 0.40; flyovers: 4.44 \pm 2.11; closest approach: 0.40 \pm 0.63, residual = 4.25 \pm 2.06. Test statistic for generalized linear mixed model (GLMM) was z ; test statistic for linear mixed model (LMM) was t .

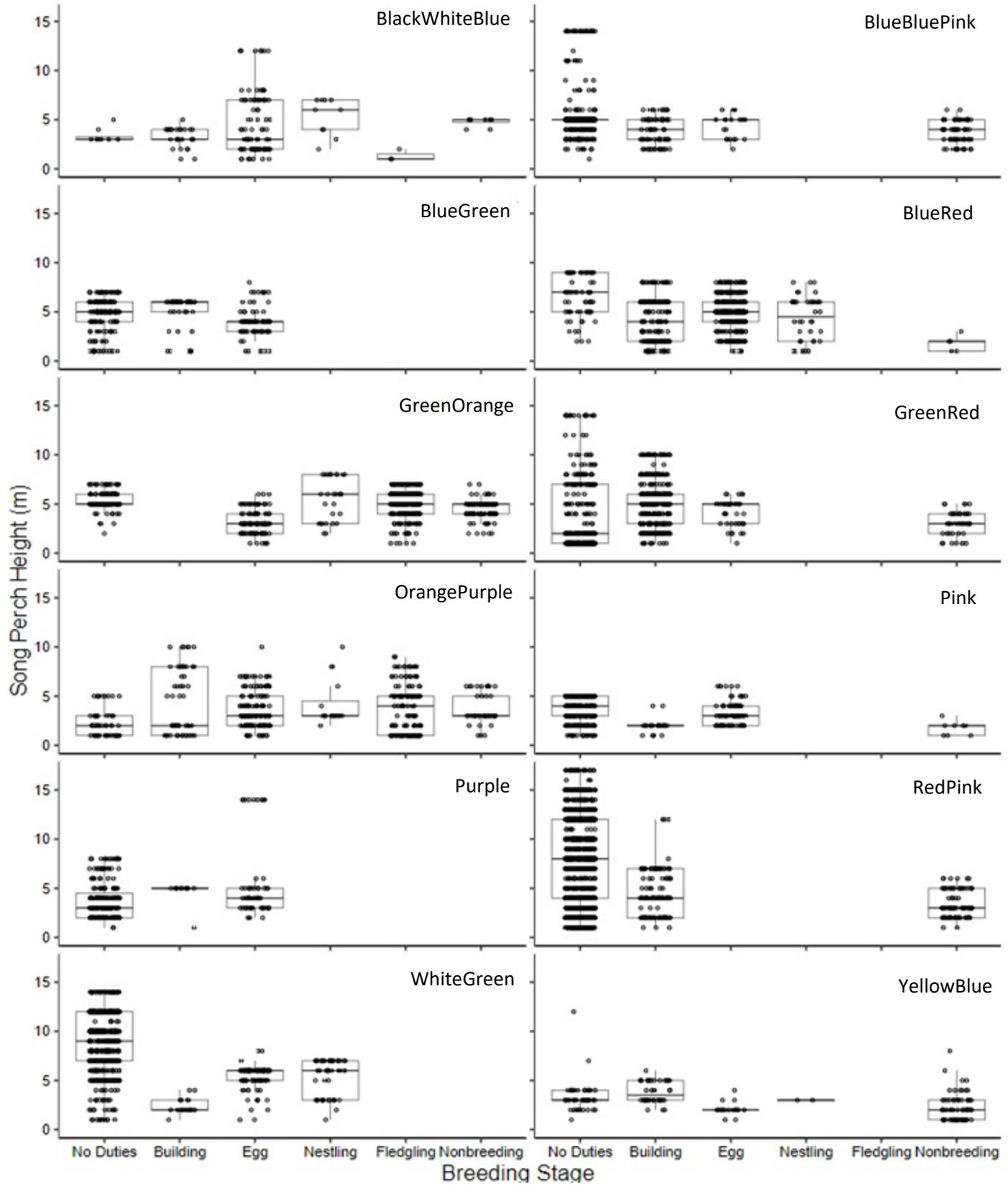


Figure 5.S1. Boxplots showing the raw data points of all song perch heights (m) per breeding stage (no duties, nest building, egg stage, nestling care, fledgling care, and non-breeding season), per male. Unique colour-ring ID for each male are shown in the top right of panels.

Woodland Photographs



Photograph of a typical invasive, woodland thicket at Shelly Hall, across a vegetable garden, where Bermuda White-eyed Vireos live. Dominant trees shown in this photograph include Brazilian peppertree (*Schinus terebinthifolia*), Chinese fan palm (*Livistona chinensis*), and fiddlewood (*Citharexylum spinosum*). Photograph by Miguel Mejías.



Photograph of a typical invasive, woodland thicket at Shelly Hall, where Bermuda White-eyed Vireos live. Dominant trees shown in this photograph include Brazilian peppertree (*Schinus terebinthifolia*) and Chinese fan palm (*Livistona chinensis*). Photograph by Miguel Mejías.



The inside of an invasive thicket at Ferry Reach Park, where Bermuda White-eyed Vireos live.

Dominant trees shown in this photograph include Brazilian peppertree (*Schinus terebinthifolia*)

and Chinese fan palm (*Livistona chinensis*). Photograph by Miguel Mejías.



Native and endemic woodland on Nonsuch Island, Bermuda, where Bermuda White-eyed Vireos live. Dominant trees shown in this photograph include Bermuda palmetto (*Sabal bermudana*), Bermuda cedar (*Juniperus bermudiana*), and Bermuda olivewood (*Elaeodendron laneanum*).

Photograph by Alison Copeland.



Inside of a native and endemic woodland in Paget Marsh, where Bermuda White-eyed Vireos live; typically, less dense than invasive thickets pictured above. Dominant plants shown in this photograph include Bermuda palmetto and cinnamon fern (*Osmunda cinnamomea*). Photograph by the Department of Environment and Natural Resources, Bermuda.

Management Plan for the Bermuda White-eyed Vireo
(*Vireo griseus bermudianus*)



Government of Bermuda

Ministry of Home Affairs

Department of Environment and Natural Resources

Management Plan for the Bermuda White-eyed Vireo (*Vireo griseus bermudianus*)

Prepared in Accordance with the Bermuda Protected Species Act 2003

Author

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Cover photo: Adult Bermudian White-eyed Vireo

Photo credit: Richard Brewer

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“To conserve and restore Bermuda’s natural heritage”

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DISCLAIMER

Management plans delineate reasonable actions that are believed to be required to manage or recover listed species. We, the Department of Environment and Natural Resources, publish management plans, sometimes preparing them with the assistance of field scientists, other government departments, and other affected and interested parties, acting as independent advisors to us. Plans are submitted to additional peer review before they are adopted by us. Objectives of the plan will be attained and necessary funds made available subject to budgetary and other constraints affecting the parties involved. Management plans may not represent the views nor the official positions or approval of any individuals or agencies involved in the plan formulation, other than our own. They represent our official position only after they have been signed by the Director of Environment and Natural Resources as approved. Approved plans are subject to modifications as dictated by new findings, changes in species status, and the completion of described actions.

Literature citation of this document should read as follows: Mejías, M. A. 2021. Management Plan for the Bermuda White-eyed Vireo (*Vireo griseus bermudianus*). Department of Environment and Natural Resources, Government of Bermuda. 36 pages.

An electronic version of this plan will also be made available at www.environment.bm



Andrew Pettit
Director
Department of Environment and Natural Resources
Bermuda Government



Date

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EXECUTIVE SUMMARY

This management plan addresses the need for actions to conserve the endemic subspecies of White-eyed Vireo (*Vireo griseus bermudianus*) on Bermuda.

Current Species Status

Legal protection for this subspecies was first granted under the Protection of Birds Act in 1975 followed by the Protected Species Act in 2003. Bermuda's White-eyed Vireos are currently listed as 'Vulnerable' under the Protected Species Amendment Order (2016). Although a local population estimate has yet to be ascertained for this subspecies, birdwatching observations (since 2011) and active leg ringing (since 2017) by the author suggests the population comprises a conservative estimate of at least 2000 individuals, across the archipelago.

Habitat Requirements and Threats

The White-eyed Vireo inhabits woodlands, copses, gardens, thickets, and overgrown fields. In precolonial times, the Bermuda White-eyed Vireo would have inhabited mixed forest stands of entirely native trees and shrubs. At present, it maintains a relatively large and stable population on Bermuda, where native forests have been largely replaced with introduced flora, forming horizontal, dense woodlands and thickets. Vegetation that supports food items, such as berries, insects, spiders, and caterpillars, are important for foraging. Branches which terminate with a stable fork that are at least 1m off the ground are crucial for nest cup placement. Important nest material includes palm fibers, bark, lichen, spider web silk, and caterpillar silk. Unfortunately, nest cup collapse is prevalent among Bermuda's vireos, suggesting suitable nesting material is a limiting factor. Adult males require a fairly large and intact area of woodland for stable pair formation and good breeding success. Although some males defend extremely fragmented and small territories, they appear less successful in attracting and keeping a mate, thus limiting their breeding opportunities. Consequentially, indiscriminate, large-scale removal of wooded habitat through human development could threaten the vireo population in Bermuda. Nest contents of White-eyed Vireos are also predated by introduced pest species e.g. the BlackRat (*Rattus rattus*), Great Kiskadee (*Pitangus sulphuratus*), Argentine Ant (*Linepithema humile*), and possibly large anoles (Dactyloidae).

Management Objective

The primary goal of this plan is to provide crucial ecological and biologically relevant data to inform management activities for the Bermuda White-eyed Vireo, as well as layout essential guidelines needed to preserve, protect, and facilitate population growth of this songbird. It is currently recognized as the only avian, terrestrial, endemic subspecies on the island and is thus of extreme conservation importance. It is with hope that this document will also encourage additional research and monitoring, mitigation of threats, and make the public aware of the

practices they can adopt that will be beneficial to our local vireo.

Management Criteria

A positive conservation status for the Bermudian White-eyed Vireo can be maintained with:

- Evidence that the local population remains stable or increases in abundance.
- Mapping vireo territories to understand home range areas necessary for survival and breeding.
- Identifying and mitigating introduced predators that threaten vireo nest success.
- Conducting population and threat assessments of other species known to provide important nesting resources for breeding vireos. E.g. Golden silk orb-weaver
- Increasing public awareness of this songbird and champion conservation efforts to protect it.

Actions Needed:

1. Estimate population size, adult survival, and juvenile recruitment, through long- term monitoring of colour-ringed vireos.
2. Map territories and site fidelity of wild, colour-ringed vireos.
3. Encourage the public to practice vireo nest predator control to improve breeding success.
4. Conduct a field study on the ecology, distribution, and threats faced by the Golden silk orb-weaver.
5. Public awareness campaign on Bermuda vireo breeding behavior, nesting threats, and habitat management.

Management Costs

The total cost of management actions cannot be defined at this point. Funding needs to be secured through non-governmental organizations (NGO's), overseas agencies, and other interested parties for implementing the necessary research and monitoring studies. Developing budgets for each action are the responsibility of the leading party as outlined in the work plan.

PART I: INTRODUCTION

A. Brief Overview

The genus *Vireo* is currently comprised of 33 recognized species distributed from Alaska to South America, including the Caribbean and Bermuda (Slager et al. 2014, Winkler et al. 2020, Mejías and Nol 2020). Most species exhibit some shade of green in their plumage, hence the Latin word “*Vireo*,” which means “I am green.” Vireos are primarily insectivorous songbirds that inhabit vegetated habitats of varying degrees of thickness, ranging from dense boreal and deciduous forests to open fields with sparse bushes, shrubs, and thickets (Mejías et al. 2020). The International Union for the Conservation of Nature (IUCN) considers the extinction risk of most vireo species as being “Least Concern” (i.e. unlikely in the near future), including the North American White-eyed Vireo (*Vireo griseus*), the primogenitor of Bermuda’s vireo.

The North American White-eyed Vireo is native to the south-eastern United States. In this region, the bird is quite cryptic and is usually heard more than seen, as it vocalizes loudly within the tangles of dense shrubs and thickets. Migratory individuals return to their northern breeding sites by mid-April (Hopp et al. 1995) before their September-October winter migration to the Caribbean and Central America. Unlike their shy mainland counterpart, Bermudian White-eyed Vireos (*Vireo griseus bermudianus*) are bold and approachable, commonly venturing outside the thicket tangles to sing from exposed perches. In Bermuda, the earliest recorded specimen dates back to 1874-75. The collector provided the following account that reemphasizes its tameness: “I have touched one with my gun in the thick bushes before it would bunch an inch” (Reid 1877). The two races also differ in that *bermudianus* spends considerably less time on the wing, preferring to move with short, flutter hops, as opposed to the long, lopping flight of North American vireos.

This island subspecies is not migratory, but rather a year-round resident. Breeding on Bermuda begins in late February, with the last chick rearing occurring in September (Mejías, unpubl. data). Although an official population estimate of Bermuda White-eyed Vireos is unavailable, their presence in almost all remaining wooded habitats suggests they are fairly abundant.

This management plan highlights the ecology and natural history of the Bermuda White-eyed Vireo, and discusses proposed necessary steps needed to protect and conserve this subspecies. More specifically, Part I briefly outlines information on taxonomy, distribution, habitat requirements, biology, and threats towards this songbird. Part II lays out the proposed management objectives and gives specific work plan actions in a step-down narrative form. Part III concludes the document with a summary table which lists the priority tasks required to complete the management objectives.

B. Taxonomy and Description of Species

Kingdom: Animalia

Phylum: Chordata

Class: Aves

Family: Vireonidae

Genus: *Vireo*

Species: *griseus*

Subspecies: *bermudianus*

Common name: White-eyed Vireo; better known in Bermuda as “*Chick-of-the-Village*,” or “*Chick-de-willy*.” Historically known as “White-eyed Greenlet,” (Jones 1859).

The White-eyed Vireo belongs to the family Vireonidae and genetic evidence suggests this species is most closely related to the Thick-billed Vireo (*Vireo crassirostris*; Slager et al. 2014, Mejías et al. 2020). Bangs and Bradley (1901) were the first to describe the Bermudian White-eyed Vireo and suggested it was a subspecies of the North American White-eyed Vireo. An updated phylogeny, where the Bermudian White-eyed Vireo was treated as a separate species, supports their hypothesis, with *V. griseus* and *V. g. bermudianus* emerging as sister species. The short branches on the phylogenetic tree between them suggests that *V. g. bermudianus* is a relatively recent arrival to Bermuda (Mejías et al.; in review). Although the North American White-eyed Vireo is a scarce, fall migrant to Bermuda, it does not breed with Bermudian White-eyed Vireos. Therefore, *V. g. bermudianus* could one day reach species-level endemism through reproductive isolation.

Physically, the Bermuda White-eyed Vireo (hereafter, “Bermuda vireo”) is a tiny songbird with green, yellow, grey, and sometimes brown, plumage colouration (Fig. 1). Total body length ranges from 115–130 mm (Mejías, unpubl. data) and body mass from 9.5–12.5 g (Table 1). Adults can be recognized by their white irises and black pupils, enclosed by lemon-yellow spectacles. They have a greyish hood, whitish throat, and a greyish-white belly boarded by yellow flanks. Their upper parts are uniform green, sometimes showing a vague yellow wash. Wings are marked with two bold yellowish-buff wing bars. Tail is green, notched, and moderate in length; undertail coverts are whitish. The Bermuda vireo has a bulbous, black, hooked-tip bill; it shares this bill shape with the rest of Vireonidae (Mejías et al. 2020). The Bermuda vireo is similar in appearance to the North American White-eyed Vireo, but *bermudianus* has noticeably longer tarsi that are black, as opposed to the bluish-grey tarsi typical of continental vireos (pers. obs). Bangs and Bradley (1901) also noted the longer tarsi in the Bermuda birds, as well as bearing shorter wings than the North American race. Table 2 summarizes morphology measurements taken from 10 Bermuda vireo specimens collected from Hamilton during the early twentieth century (Bangs and Bradley 1901). The wing chord, tarsus length, and bill length (i.e., “exposed culmen”) measurements of present-day are congruent with historical measurements (see Tables 1 and 2; Mejías, unpubl. data).

Bermuda vireo fledglings are similar in appearance to adults, with the exception of a dark iris and less brightly coloured plumage (Fig. 2). Compared to adults, many physical features of young Bermuda vireos are muted. Most obviously, young birds lack the

quintessential white eyes of adults. With maturity, the eye colour gradually changes from coffee-brown, to dark grey, to greyish-white, to pure white, from 1 year (Mejías, pers. obs.) to two (Pyle 1987). The spectacles and flanks of juvenile vireos are also drab yellow compared to adults.



Figure 1: Photograph of an adult Bermuda vireo. Note the diagnostic white eye from which the species' common name is derived. Other noteworthy traits include the bright yellow spectacles, flanks, greenish upperparts, and two bold buffy-yellow wing bars. Photographed by Luke Foster.



Figure 2: Photograph of a juvenile Bermuda vireo. Photographed by Richard Brewer.

Table 1: Morphology measurements taken from Bermuda vireos captured and colour- ringed in 2018. *Bill length represents exposed culmen.

Body Mass (g)	Wing Chord (mm)	Bill Length* (mm)	Tarsus Length (mm)
12.5	57	8.9	24.7
11	60	9.4	26
9.5	60	9.4	24.9
11.5	60	9.2	23.3
11	59	10.8	22.4
11.5	61	9.8	23
12	62	11.2	25.7
11.5	62	9.4	24.7
12.5	61	10.2	23.9
11	60	9.6	25.1

Table 2: Summary of historical morphology measurements taken from Bermuda vireos.

Measurements.

No.	Sex.	Wing.	Tail.	Tarsus.	Exposed Culmen.
39131 Mus. Comp. Zoöl. Type.	♂	58	46	20.4	10.6
1 Bradlee Coll.	♂	59	46.5	20.4	11
2 "	♂	59	47	20.2	11
3 "	♂	58	45	20.6	10.4
4 "	♂	59	46.5	20.2	10.4
8 "	♂	59.5	47	20.2	10.4
10 "	♂	58	45	21	10.6
11 "	♂	59.5	47	20.4	10.8
4162 Bangs Coll.	♂	59.5	47	21	11
4161 "	♂	59	48	21	10.6

Vireo vocal displays are the loudest and most conspicuous of any of Bermuda's native terrestrial avifauna. The primary song of this species, performed only by males, is often described as "explosive" (Bradley 1980, Borrer 1987), with song elements comprised of chips, buzzes, and whistles uttered rapidly. A Bermudian rendition of this song, "Chick-of-the-Village," gives the bird its nickname. Additional song interpretations include "ginger-beer-quick" and "chick-choo-willio" (Bangs and Bradley 1901). If compared to the English language, each song can be thought of as a single sentence, with each song having a fixed/predictable structure lasting about one second long. Male Bermuda vireos appear to have a repertoire of about 7-10 songs (Mejías, unpubl. data). Males use these songs for mate attraction and territory defense (Bradley 1987, Mejías, unpubl. data). A second vocal display typical of this species are scolding calls, which are nasally, harsh, whining notes that are uttered either singly or in quick succession. These calls are used by both sexes, usually during territorial conflicts, perceived threats, and even directed at birdwatchers who use "pishing" calls (Mejías, pers. obs).

C. Current Status

Subspecies Range

The Bermuda vireo is only found on the Bermuda archipelago. Although sedentary like the White-eyed Vireo subspecies in the southern United States and Mexico (Hopp et al. 1995, Somershoe et al. 2005), *bermudianus* likely descended from the North American, migratory subspecies, *V. griseus griseus*, which breeds in the northern states during the spring and summer (Nolan and Woldridge 1962, Somershoe et al. 2005) and migrates to the Caribbean and the Yucatan Peninsula for the winter (Hopp et al. 1995, Somershoe et al. 2005; Fig. 3). Bermuda's proximity to the eastern seaboard makes the island an occasional stopover site for migrant vireos (Fig. 3).

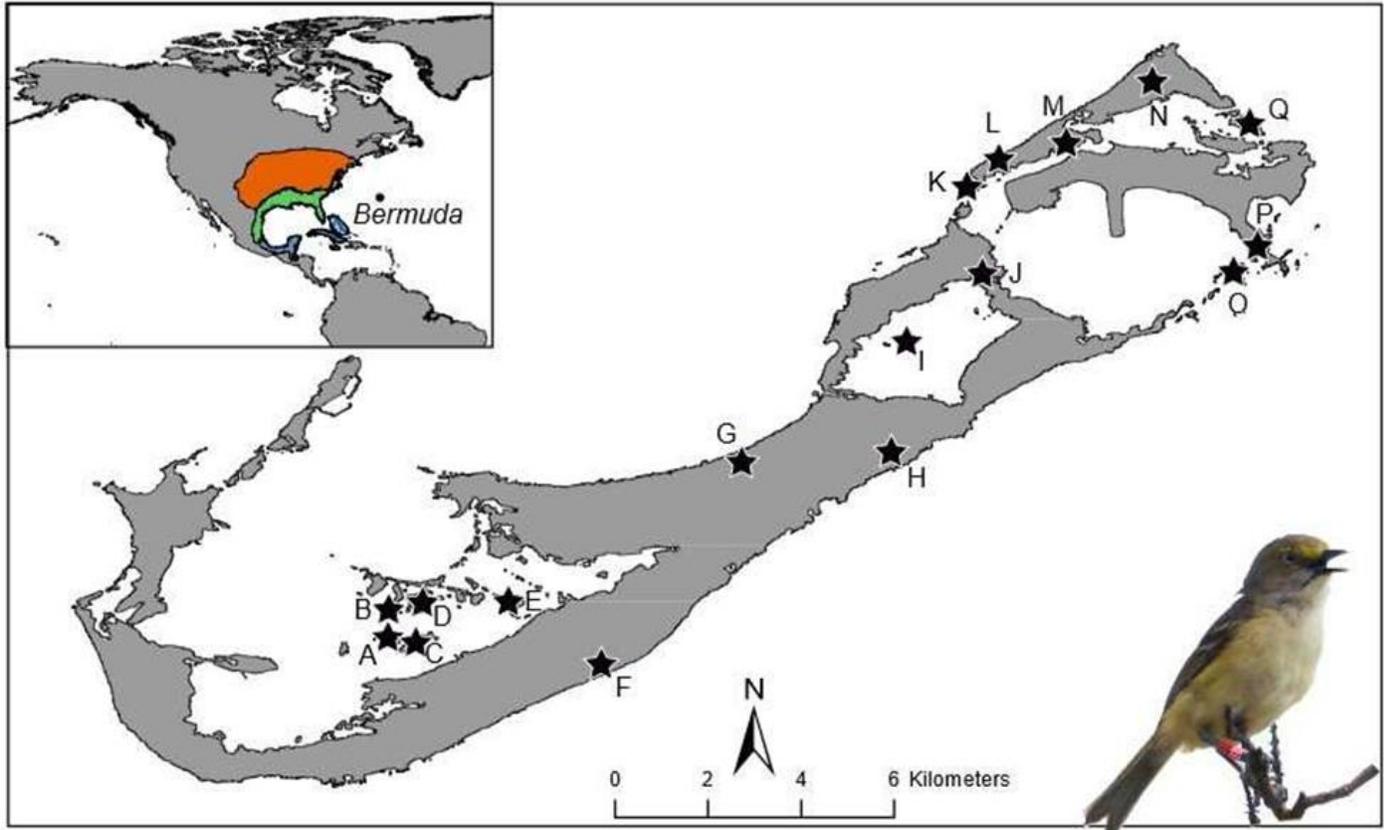


Figure 3: A map of the Bermuda archipelago depicting all sites (“stars”) where Bermuda vireos have been captured and colour-ringed, between 2015 and 2021: A: Burt’s Island (N= 3 birds), B: Gamma Island (2); C: Darrell’s Island (18); D: Port’s Island (16); E: Hinson’s Island (17); F: ABS Nature Reserve (2); G: Oceanview Golf Course (8); H: Spittal Pond (16); I: Trunk Island (3); J: Blue Hole/Tom Moore’s Tavern (7); K: Ferry Reach Park (102); L: Lover’s Lake (5); M: BIOS (3), N: St. George’s Golf Course (34); O: Nonsuch Island (6); P: Cooper’s Island (1) and Paget Island (4). Note, while the Bermuda vireo is indeed found across the archipelago, stars only denote sites where birds were captured and colour- ringed. The inset map depicts the ranges of the North American White-eyed Vireo; orange represents the breeding range of migratory individuals, green represents the year-round range of non-migratory individuals, and blue represents the wintering range of migratory individuals. Photo of colour-ringed Bermuda vireo by Neal Morris.

Local Distribution

Historical Distribution

Historical records suggest the Bermuda vireo was abundant island-wide. Reid (1877) described it as “one of the commonest resident Bermuda birds.” It was often seen foraging 3-12 feet from the ground among cedars, mangroves, “holly” pomegranate, and lemon trees, with most sightings occurring in cedars (Reid 1877). Jones (1859) described it as “found in abundance all the year round.” Bowditch (1904) echoed these testaments, stating “this bird ranks with the Cardinal and the Catbird in point of numbers; everywhere one goes, he hears its characteristic song, translated into ‘chick-of-the-village’ by the negroes.” Even towards the end of the 20th century, which marked a drastic increase in human development and increased forest fragmentation (Dobson 2002), this tiny vireo was still considered abundant island wide by local birdwatchers and naturalists (Amos 1991).

Contemporary Distribution

The Bermuda vireo can be readily found in almost all wooded areas across mainland Bermuda and offshore islands; some of these sites allowed several to be readily captured, colour-ringed, and studied (Fig. 3). It is easily the most abundant native songbird on the island, with local birdwatchers reporting sightings of them year-round (eBird, Bermuda sightings database). They are most abundant in large, intact wooded areas, such as Ferry Reach Park, Spittal Pond, Hog Bay Park, and Southlands (Mejías, pers. obs). In contrast, they appear virtually absent in the center of the heavily developed city of Hamilton and city parks, but become readily apparent in wooded areas on city boundaries, and beyond (Mejías, pers. obs).

Species Protection

Following IUCN criteria, the Bermuda White-eyed Vireo is listed as ‘Vulnerable’ (D1 + 2) under the Protected Species Amendment Order (2016). Current legal protection is provided by the Protected Species Act (2003) which considers the willful destruction, damage, removal or obstruction of habitats, and the taking, importing, exporting, selling, purchasing, or transporting this species an offence. Offenders are liable to a fine of up to

\$25,000 or two years imprisonment.

Habitat Protection

Some woodlands inhabited by vireos occur in Government owned nature reserves and parks and are therefore afforded protection under the Bermuda National Parks Act (1986). Others occur within privately owned lands that have varying levels of protection depending on how they are zoned by the Department of Planning (i.e. Nature Reserve, Woodland Reserve, and Open Space Reserve).

D. Ecology

Habitat Requirements

The White-eyed Vireo nests within thickets as well as in sparse, shrubby, open habitat (Winkler et al. 2020). In North America, this species is found nesting in scrubby, second growth forest and marsh edge, with birds sometimes distributed patchily (Bradley 1980). Continental vireos are considered habitat generalists (Peake and Ritchison 1998, Kovar 2015). Prior to human settlement, the Bermuda vireo would have inhabited woodlands and thickets comprising mostly native, evergreen flora. A typical precolonial woodland would have had Bermuda Cedar (*Juniperus bermudiana*), Bermuda Olivewood (*Elaeodendron laneanum*), Bermuda Palmetto (*Sabal bermudana*), Southern Hackberry (*Celtis laevigata*), and Yellowwood (*Zanthoxylum flavum*) as canopy trees, and shrubs such as Bermuda Sedge (*Carex bermudiana*), Bermuda Snowberry (*Chiococca alba*), and Bird Pepper (*Capsicum baccatum*) dominating the understory (Britton 1918, Bermuda Plant Finder 2016). In present-day Bermuda (21st century) the majority of the woodlands and thickets across the island are second growth forests made almost entirely of introduced and invasive trees. Arguably the most drastic changes in Bermuda vireo habitat was the loss of the Bermuda Cedar dominated forests during the middle of the 20th century, following excessive logging and accidental introductions of two scale insects (Challinor and Wingate 1971, Tucker 1970). Woodland species now include Casuarina (*Casuarina equisetifolia*), Brazilian Pepper (*Schinus terebinthifolia*), Chinese Fan Palm (*Livistona chinensis*), and Allspice (*Pimenta dioica*) as canopy trees, and Asparagus Fern (*Asparagus densiflorus 'Sprengeri'*), Asparagus Wedding Fern (*Asparagus setaceus*), and sapling Suriname Cherry (*Eugenia uniflora*), as the lower shrubby layer. Bermuda vireos are also habitat generalists, and are found nesting and defending territories comprised largely of introduced trees and shrubs (Mejías and Nol 2020). Bermuda Cedar and Southern Hackberry are the most commonly used native nesting trees, whereas Brazilian Pepper and Suriname Cherry are the favoured introduced trees (Mejías, pers. obs).

Bermuda vireo territories require sufficient size to have an ample supply of plants that provide food and nesting material. Preliminary territory mapping revealed neighboring males occupy well-defined, largely non-overlapping territories, that vary in size (Mejías and Musiuk unpubl. data; Fig 4 and 5). These territories are defended by the males year-round. It is also important for the tree species that make up the territory to attract sufficient insect prey items and produce adequate berries and fruits for consumption (see “Diet and Feeding” below for more details). Similarly, various tree species that provide nesting material and attract silk-producing spiders and caterpillars (see “Reproduction” below for more details) are essential for nest construction. For these reasons, a mixed woodland would be more productive than a monoculture woodland.

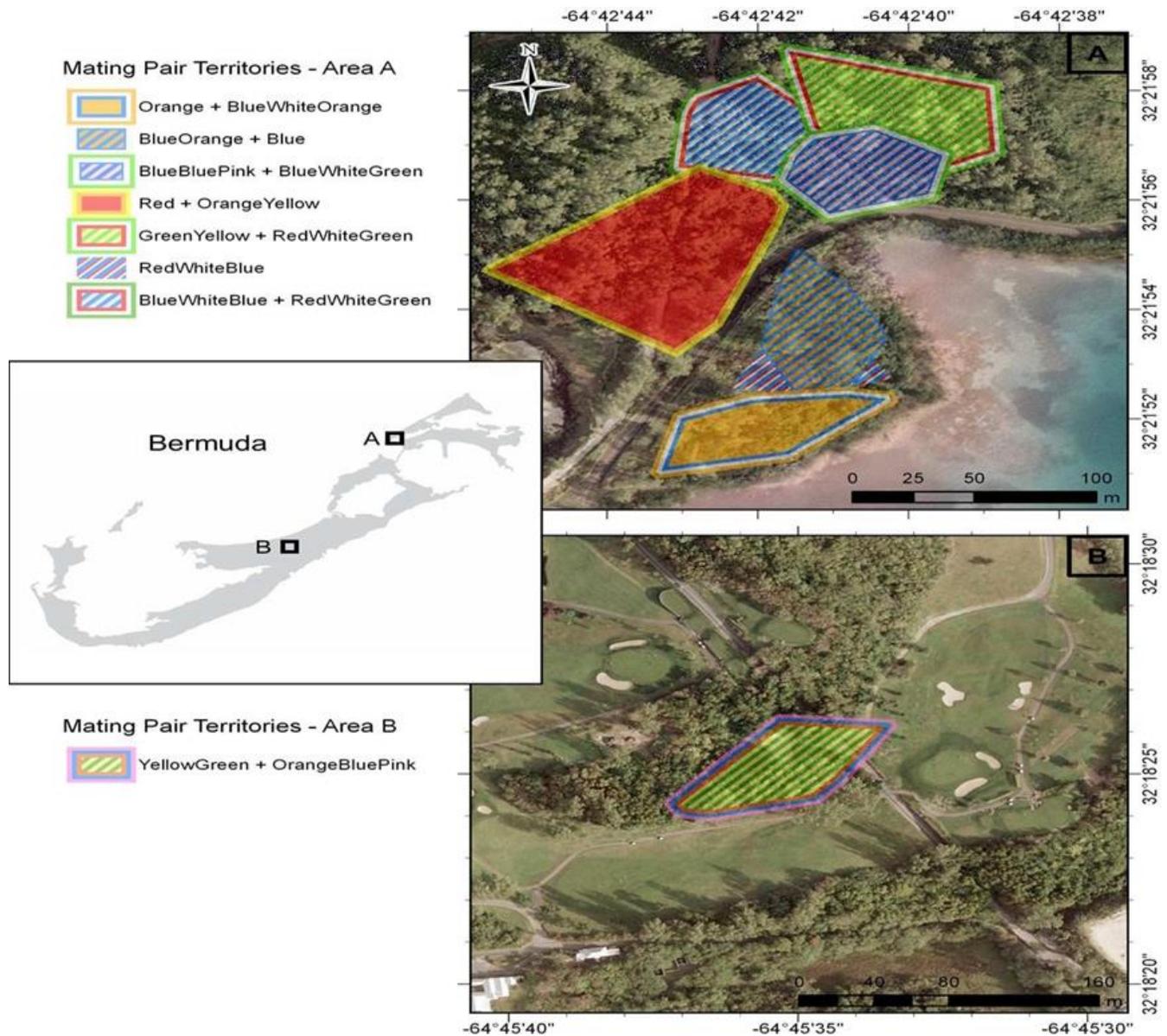


Figure 4. Preliminary territory data of 8 neighbouring colour-ringed male Bermuda White-eyed Vireos at Ferry Reach Park (top panel) and 1 male at Oceanview Golf Course (bottom panel) studied between 2016 and 2017. GPS points were collected with a Garmin handheld GPS unit (3m accuracy) corresponding to multiple sightings of banded individuals.

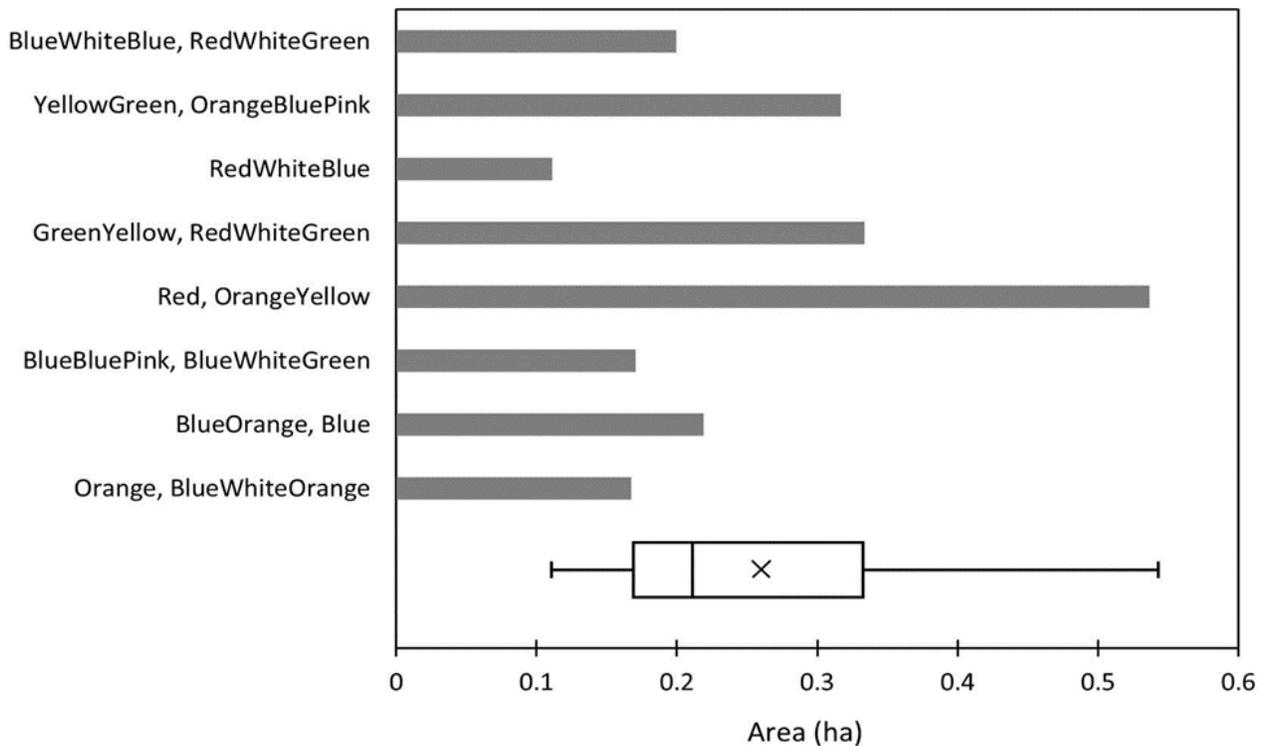


Figure 5. Histogram depicting territory size of the same 8 colour-ringed male Bermuda White-eyed Vireos in Fig. 6. Ring colour on the left and right of comma represent banded male and female vireos, respectively. Male (Red + White/Blue) had the smallest territory, and was the only male who was unable to attract a female. The “X” marks the average territory size among males.

Reproduction

Bermuda vireos can usually be found travelling in pairs, with both sexes sometimes shadowing one another year-round. Unpaired males generally ascend to higher perches and sing tirelessly until paired, at which point males sing primarily in the understory (Mejías, unpubl. data). Their nesting season spans February — September, marking the start and end of nest building and fledgling feeding, respectively (Mejías, unpubl. data). Local colour-ringing revealed that vireos can breed as early as their first year of life and can live to at least 6 years of age. Their neat, bowl or cup-shaped nests are constructed with plant matter and trash, which carry their small (length: \bar{x} = 18.9 mm, width: \bar{x} = 14.5 mm, n = 2 eggs, 1 clutch), white and brown eggs (Fig. 6). Bermuda vireos appear to produce only one brood a year, although pairs have been observed building as many as 5 successive nest cups in a season, each following nest failure (Mejías, unpubl. data). Their nest construction usually begins with the male securing the first bit of nest material, most commonly a piece of polyfill cotton (Fig. 7), suggesting the male selects the nest-site. Both sexes then begin adding bits of plant matter to build an outer wall, comprised largely of loose tree bark and leaves collected from plants, like Bermuda Palmetto,

Allspice, and Cow Cane (*Arundo donax*), and then dotted with tufts of green moss and lichen (*Ramalina denticulata*), presumably for camouflage. Silk collected from spiders and caterpillars help bind this nest material together. The incredibly durable webbing from the Golden silk orb-weaver, known locally as the “Hurricane Spider,” was once commonly used in nest construction (Wingate, pers. comm). There was also an account of a Bermuda vireo within the Hungry Bay mangrove trees with thick webbing (likely from the Golden silk orb-weaver) completely covering its right eye (Bowditch 1904). Finally, the nest is lined with fine, reddish-brown straw fibers, collected from the trunk base of both Bermuda Palmetto and Chinese Fan Palm, which the vireos smooth out via foot stomping. Peake and Ritchison (1998) outline three important criteria for nest cup placement for continental White-eyed Vireos, and these are also practiced by Bermudian vireos (Mejías, pers. obs): (1) nests are suspended at least 1 m of the ground, (2) branches of nest trees should terminate with a strong, “Y-shaped” fork that can support a hanging nest cup, and (3) some degree of foliage concealment for the nest cup. Their tendency to use almost any tree species that exhibit these characteristics undoubtedly favoured their survivability on the heavily developed and populated Bermuda archipelago.

With the exception of fledgling care, breeding data is based on a subset of the author’s doctoral thesis. Nest construction takes about 3-12 days ($n = 4$ nests, $\bar{x} = 7$ days), with the male often quitting during the final few days of nest building, where he closely shadows the female on collecting trips, whilst constantly flicking his wings (Mejías, pers. obs); wing-flicking is recognized as a copulatory display in some songbirds (Dunham 1964, Brooker and Saffer 1996). Bermuda vireos may abandon a nest if it’s in close proximity to busy foot traffic or if the nesting pair discovers someone too close to their nest, although abandonment appears less likely when eggs or chicks are present (Mejías, pers. obs.). Egg laying usually begins 3-4 days after nest cup completion. Clutch size ranges from 1-4 eggs, with 3 being the average. Both sexes partake in incubation (about 14 days, $n = 2$ clutches, $\bar{x} = 14$ days) and chick rearing in the nest (9-12 days, $n = 2$ broods, $\bar{x} = 11$ days). After fledgling, the male and female split the brood, the former often looking after most of the young (as many as 3 at once), and proceed to feed them in different parts of the territory (Mejías, pers. obs). While males usually feed their fledglings inside his territory, females commonly guide their young beyond her mate’s boundaries, usually feeding them inside neighbouring territories (Mejías, pers. obs). At this stage, fledglings can be heard giving insistent begging calls, which sound like a primitive version of this subspecies’ scolding calls. Throughout fledgling feeding, adult plumage becomes oily and unkempt, as feeding duties take precedence over preening (Mejías, pers. obs). Parents rear fledglings for 26 – 57 days ($n = 5$ feeding fathers, $\bar{x} = 41$ days) before young disperse (several kilometers) from natal territories.



Figure 6. Photographs of Bermuda White-eyed Vireo nest (left) and a 3 egg clutch from a different nest cup (right). The nest cup is suspended from an Allspice (*Pimenta dioica*) tree.



Figure 7. A piece of polyfill debris suspended from a Brazilian Pepper (*Schinus terebinthifolia*) branch by an unpaired male Bermuda vireo, decorated with the lichen, *Ramalina denticulata*. This is likely a “bachelor pad” nest that unpaired males sometimes build to attract a prospecting female.

Diet and Feeding

Continental White-eyed Vireos in the breeding season mainly consume insects and spiders (Nolan and Wooldridge 1962). During the non-breeding season they switched to a primarily plant-based diet (Greenberg et al. 1995). Similarly, Bermuda vireos in the breeding season primarily eat insects and spiders, with their most common prey being bright, lime green caterpillars (Fig. 8). This is most notable during the chick-rearing period, when their facial feathers become soiled, matted, and stringy from the bodily fluids of pulverized caterpillars (Mejías pers. obs). Additional spring and summer prey items include small flies (Arthropoda), spiders (Arthropoda), dragonflies (Anisoptera), moths (Lepidoptera), anoles, and nestling fecal sacs (Mejías pers. obs). Bermuda vireos locate their prey by methodically peering at the surface and undersides of branches, twigs, and leaves, while busily flutter-hopping. They primarily hunt amongst perches 2-5 meters above ground (Mejías pers. obs). This vireonid is quite versatile in its foraging behaviour. They seize aerial prey with quick bill snaps, a sound reminiscent of a “twig snap,” either by extending their head whilst perched, hovering in mid-air, or in passing

flight between perches. Foraging birds may sometimes abruptly fall several meters to a lower perch following an aerial bill snap. Larger prey items (i.e., moths, caterpillars, and anoles) are often held in the bill and beaten against a hard perch or secured between the feet where they are pecked and dismembered prior to consumption. Bermuda vireos also capture prey by hanging from them with just their bill (Fig. 8). A small Jamaican Anole (*Anolis grahami*) on the underside of a branch was seen captured in this manner, where the vireo swung from the anole's neck, until the lizard lost its grip, and the two tumbled to a lower branch, with the vireo landing upright, and proceeded to peck and dismember the lizard held between its feet, prior to feeding it to a fledgling (Mejías pers. obs). In the winter, Bermuda vireos incorporate more plant matter in their diet. Reid (1877) reports them eating the white berries of "Tournefortia" and Bird Pepper (*Capsicum baccatum*). Fruits from Bermuda Snowberry, Poison Ivy (*Toxicodendron radicans*), Turkey Berry (*Callicarpa americana*), and Brazilian Pepper are likely additional sources of winter food.



Figure 8. Photographs of Bermuda vireos consuming caterpillars. The bright green species depicted in the left panel is likely a Green Looper (*Chrysodeixis eriosoma*). Right panel depicts the “hanging” prey capture method this subspecies uses to secure wedged or secured food. Photographs by Richard Brewer.

E. Current Threats

Local

The Bermuda vireo is largely threatened by anthropogenic factors. As early as 1982, new housing units were erected at a rate of 300 units/yr, making present-day Bermuda, whose population surpassed 62,000 people, one of the most densely populated oceanic islands in the world (1,275 people/km²; Wingate 1990, Dobson 2002). The replacement of wooded areas with urban development has resulted in approximately 14% of the archipelago being covered by impermeable surfaces (Dobson 2002). Consequently, development has diminished and fragmented woodlands the vireo requires for foraging, shelter, and reproduction (Fig. 9).

Introduced nest predators threaten eggs and developing chicks (Mejías, unpubl. data). For example, Argentine Ants (*Linepithema humile*) can devour down-free nestlings. The Great Kiskadee (*Pitangus sulphuratus*) was observed attacking a Bermuda vireo brooding recently hatched nestlings, and the nest was found destroyed a few days later. The Black Rat (*Rattus rattus*), a common predator of seabird eggs and chicks in Bermuda (Mejías et al. 2017), were sighted frequently on the ground directly underneath vireo nests, and nestlings often disappeared a few days following daytime rat sightings. Large Antiguan Anoles (*Anolis leachii*) occasionally approached vireos inside nest cups, causing the latter to spread its wings and tail, but have yet to be seen consuming nest contents; this anolis lizard has been documented eating Eastern Bluebird (*Sialia sialis*) eggs in Bermuda (Dobson, pers. obs.).

Lastly, nest collapse was observed to be fairly high, with almost every pair studied experiencing at least one nest cup falling apart throughout each breeding season. At no point did any nesting pair attempt to repair damage after nest cup completion. Observed nest collapse may be because of insufficient nesting material availability, specifically the scarcity of the highly durable webbing from the Golden silk orb-weaver, which was not found in any of the collected nest cups (~ 50 nests). Ironically, this same webbing has led to the ensnarement of Bermuda vireo fledglings (Reid 1877), which would undoubtedly kill the young birds if they couldn't escape. Direct sources of mortality of adults are scant at this time, although their tendency to remain in higher perches among dense thickets, as opposed to feeding openly on the ground, appears to greatly reduce their vulnerability to cats and wintering raptors.



Figure 9. A bulldozed upland hillside at White Crest Hill in Hamilton Parish where Bermuda vireos are known to abundantly occur.

F. Current Conservation Actions

Local conservation effort towards the Bermuda vireo has been sporadic and scant. In 1972, Dr. David Wingate captured and translocated several individuals in an attempt to reestablish breeding pairs on the recently reforested Nonsuch Island (Wingate 1990). In 2015 a local birdwatcher, Paul Watson, began colour-ringing Bermuda vireos under license from the Department of Environment and Natural Resources in an effort to understand their survival and site fidelity. In 2017 a doctoral study investigating their singing behaviour, breeding biology, and nesting threats was initiated by the author of this management plan. Indirectly, the Bermuda vireo has received long-term benefits through habitat protection granted by the National Parks Act (1986) which has preserved various tracts of woodland across Bermuda.

PART II: MANAGEMENT

A. Management Goal

The ultimate goal of this management plan is to promote the persistence and population growth of the only remaining endemic, terrestrial, subspecies of bird on the Bermuda archipelago, the Bermuda White-eyed Vireo. This plan presents crucial information on the ecology, natural history, and threats pertaining to the Bermuda White-eyed Vireo, and this data should prove useful in driving proactive measures to protect this vireonid. This can ultimately be achieved by doing a census study on Bermuda vireo numbers, obtaining legislative protection for currently unprotected wooded sites known to support vireos, making landowners aware of available nest predator control resources, proposing alternative invasive tree management practices, and increasing the general public awareness of this endemic subspecies.

The short-term (5 years): To expand capture and colour-ringing field survey sites of adult and juvenile Bermuda vireos and perform a population assessment based on these marked birds. Identify privately owned large tracts of woodland (> 0.5 ha) capable of supporting multiple vireo pairs and liaise with landowners on habitat management practices that will benefit the vireo. Begin advocating for better nest predator control and woodland management among homeowners. Initiate field studies investigating t

he abundance, distribution, and threats facing the Golden silk orb-weaver in Bermuda, whose strong webs are likely a limiting resource for nest building vireos. Finally, spread local awareness of this vireonid through public lectures and local advertisements.

Long-term (20 year): Monitor and publish findings on the stability, size, and distribution of the Bermuda vireo population across the island. Establish legislative protection for large, privately owned woodlands. Using field data collected during the short-term period, produce a report on the biology, abundance, and threats, facing Bermuda's Golden silk orb-weaver, as well as any interactions between this arachnid and Bermuda vireos. Assess Bermuda vireo nesting success in areas where predator control efforts have been implemented annually to establish how it varies from unmanaged sites. Finally, continue to present current data pertaining to the ecology, population status, threats, and conservation efforts aimed at this subspecies.

B. Management Objective and Criteria

Management Criteria

A positive conservation status for the Bermudian White-eyed Vireo can be maintained with:

- Evidence that the local population remains stable or increases in abundance.
- Mapping vireo territories to understand home range areas necessary for survival and breeding.
- Identifying and mitigating introduced predators that threaten vireo nest success.
- Conducting population and threat assessments of other species known to provide nesting resources for breeding vireos. E.g. Golden silk orb-weaver
- Increasing public awareness of this songbird and champion conservation efforts to protect it.

Actions Needed:

1. Estimate population size, adult survival, and juvenile recruitment, through long-term monitoring of colour-ringed vireos.
2. Map territories and site fidelity of wild, colour-ringed vireos.
3. Encourage the public to practice vireo nest predator control to improve breeding success.
4. Conduct a field study on the ecology, distribution, and threats faced by the Golden silk orb-weaver.
5. Public awareness campaign on Bermuda vireo breeding behavior, nesting threats, and habitat management.

This management plan acknowledges both the straightforward and difficult efforts deemed necessary to ultimately favour population stability and growth of the Bermuda vireo. Traits that facilitate their management include their present-day island-wide abundance, tame nature, conspicuous vocal displays, catchability with mist nets, and their willingness to breed in a broad diversity of tree species, both native and introduced. In contrast, several aspects of their breeding present significant management obstacles. Not only are their nests extremely small and cryptic, they are prone to human-induced abandonment, and have contents that are vulnerable to a diverse array of superabundant, introduced predators that overlap extensively with breeding sites. Despite these challenges, if the proposed actions in this management plan are implemented, even at suboptimal levels, it will undoubtedly favour the persistence of nesting Bermuda vireos across the archipelago.

C. Tools Available for Strategy

Mist Netting and Banding/Ringing

Mist netting is a capture technique that uses a fine meshed net suspended between two tall poles. Mist nets can be raised in a narrow clearing in a wooded habitat or in a sparse, open area, depending on the habitat of the target species. Ideally, mist nets are installed in places where the environmental background and lighting conditions reduce visibility of the mesh to target birds. Mist nets are lined with shelves or “pockets” where captured birds fall and hang from (Fig. 10). Birds can either be captured passively, by waiting for individuals to fly into the net, or, actively, by placing a speaker and audio device that broadcasts the songs/calls near the net to lure birds in; both mechanisms have proven to be extremely effective in capturing Bermuda vireos (Mejías, pers. obs.). The latter method, however, is more likely to skew capture rate towards male Bermuda vireos, because they respond more aggressively towards playbacks of the species’ song and calls (Mejías, unpubl. data). It is imperative that active mist nets are monitored closely so that captured birds can be readily and safely removed, thereby reducing stress and risk of injury. A pair of bird banding/ringing pliers should be used to fit a single metal identification ring on one leg, as well as the addition of colour-ring(s) on either leg for individual recognition from afar (Fig. 10).



Figure 10. Bermuda vireo captured via mist netting (left) and banded (right).

The uttermost care should be taken to ensure the leg colour ID sequence is not repeated for individuals belonging to the same species. Colour-rings are tiny, hollow, plastic cylinders made of celluloid or darvic. Caution should be taken when stacking colour-rings onto birds to avoid tarsal swelling; this symptom was always seen with the stacking of darvic colours, not celluloid (Mejías, pers. obs.). Leg irritation can be greatly reduced by using one colour ring, per leg. Mist netting and ringing of birds requires extensive training from an experienced and licensed bird bander. Experienced individuals may apply for a local bird banding permit at the Department of Environment and Natural Resources. This

permit will be necessary to purchase mist nets, birding banding pliers, and leg rings from an overseas supplier. There is an extensive literature on the methodology on safely mist netting and ringing captured songbirds (see Stamm et al. 1960, Dunn and Ralph 2004, Avinet Research Blogs 2019).

Point Count Surveys

Point counts are another standard methodology used to census wild birds during which an observer stands in a single spot for a specific time period and records the presence and numbers of individuals and species seen or heard within a specified radius (Hutto et al. 1986, Leu et al. 2017, Campomizzi et al. 2020). Despite its popularity in field ornithology, the technique comes with inherent biases and limitations (see Simons et al. 2009). For example, although radius point counts were effective in estimating Bermuda vireo abundance in wooded habitats across the island (Mejías and Nol 2020), most individuals were detected by their song, a signal only produced by males, thus underestimating the species' true abundance by excluding females. Furthermore, their singing rate changes with respect to whether or not males are paired with a female (Mejías, unpubl. data). In light of this limitation, radius point counts should be combined with other surveying techniques in order to get a more accurate abundance estimate for this subspecies. Nonetheless, point counts are, at the very least, appropriate for presence and absence vireo surveys.

Nest Predator Control

At least three predators have been recognized as threats to Bermuda vireo nests: Argentine Ant, Black Rat, and Great Kiskadee. All are introduced pests. Although these threats can be readily managed on small, wooded, offshore islands where Bermuda vireos nest, their superabundant presence on mainland Bermuda makes total eradication highly improbable. Nonetheless, limited measures can be taken to ease predation pressure on mainland nesting pairs. Both ants and rats can be controlled with poison bait. The number of poison bait required will ultimately depend on the size of the wooded areas, as well as the estimated abundance of vireos, rats, and ants. Inquiries about the handling, distribution, and purchase of rodenticides should be directed to Bermuda Vector Control. Ant poisons can be locally purchased from a variety of hardware stores. Controlling kiskadees will prove to be more challenging. Live capture using letterbox (aka ladder) traps has shown some promise and should be used in the future.

Bermuda Audubon Society and Bermuda Natural History Museum

Additional information and live encounters of the Bermuda vireo can be acquired through the Bermuda Audubon Society. This local charity hosts several birdwatching, photography walks, and lectures throughout the year, both of which provide ideal opportunities to observe the Bermuda vireo in their habitat. Experienced, local birders also routinely attend these events, serving as an additional source of information on the local vireo. The Bermuda Natural History Museum is also an excellent resource for local publications on the Bermuda vireo, as well as study skins available for research purposes.

E. Step-down Narrative of Work Plan

Abbreviations used in Section E and Part III:

DENR – Department of Environment and Natural Resources

BAMZ – Bermuda Aquarium Museum and Zoo

BAS – Bermuda Audubon Society BVC – Bermuda Vector Control BBB – Buy Back Bermuda

MM – Miguel Mejías

The actions needed to achieve effective management are as follows:

1. *Estimate population size, adult survival, and juvenile recruitment, through long-term monitoring of colour-ringed vireos.*

Actions proposed:

- Mist net and colour-ring adult and fledgling Bermuda vireos,
- Revisit field sites at least twice a year, once in the breeding season and once in the non-breeding season, and document recaptured or re-sighted vireos,
- Map general localities of where colour-ringed vireos were captured, recaptured, and re-sighted,
- Encourage public to report or photograph encountered colour-ringed vireos.

Work Team: MM and DENR

Team Leader: MM

Assistance: BAMZ, volunteers, graduate students, visiting researchers

Outputs: A long term dataset comprised of recaptured and re-sighted colour-ringed vireos which can be statically analyzed for estimates of population abundance and survival.

List of equipment required: Vehicle to get to sites, mist nets, metal and colour rings, banding pliers, breathable, cotton bags to hold captured vireos, binoculars, and a computer with appropriate statistical/survival analysis software installed.

2. *Map territories and site fidelity of wild, colour-ringed vireos.*

Actions proposed:

- Visit all field sites several times a year, and use a handheld GPS unit to collect GPS points where colour-ringed birds were seen/recaptured,
- Plot these GPS points onto a map and calculate territory sizes,
- Monitor breeding activities of individuals being mapped.

Work Team: MM, DENR, BAS, BAMZ

Team Leader: MM

Assistance: BAMZ, volunteers, graduate students, visiting researchers

Outputs: A report containing a series of maps outlining site fidelity, territory size, and temporal changes in said territory size, and its implications on nesting Bermuda vireos.

List of equipment required: A vehicle to get to study sites, a handheld GPS (Garmin units, with ~3m accuracy are sufficient), a physical or digital fieldbook, binoculars, and a computer with appropriate mapping software.

3. *Encourage the public to practice vireo nest predator control to improve breeding success*

Actions proposed:

- Promote effective methods of predator control on private properties to reduce rat and ant abundance (e.g. poisons and trapping)
- Promote proper sanitation methods at home by reducing shelter and food sources available to rats and ants,
- Discuss and collaborate with BVC to achieve realistic poison control efforts, for a property,
- Follow-up with landowners on whether or not they still detect rats and ants, after practicing predator control,
- Monitor the number of vireo fledglings heard or seen (a measure of vireo productivity) in the property, before and after predator control efforts.

Work Team: MM, DENR, BVC

Team Leader: MM, DENR

Assistance: BAS, landowners, hired groundskeepers of managed sites

Outputs: The extermination of rats and ants on small, wooded, offshore island residential properties that also support breeding Bermuda vireos. A reduction in predation on the Bermuda mainland. A revitalized obligation and appreciation in the steps island residents can take to protect our local vireo, and other native species.

List of equipment required: Binoculars, physical or digital fieldbook, rat/ant poison, poison bait boxes, mist nets, and letterbox traps.

4. *Conduct a field study on the ecology, distribution, and threats faced by the Golden silk orb-weaver, whose strong webs were known to be used by nesting Bermuda vireos, and is likely a limited resource, due to a perceived drastic decline in this local arachnid.*

Actions proposed:

- Encourage the general public to report sightings of Golden silk orb-weavers,
- Conduct field surveys to quantify the abundance and distribution of Golden silk orb-weavers across the island,
- Use field observations to document habitat preference, interactions with nesting vireos, and threats

Work Team: DENR and MM

Team Leader: MM

Assistance: General public, local school students, volunteers, graduate students, visiting researchers.

Outputs: A report outlining the status of the Golden silk-orb-weaver, and its ecological interactions with other species,

especially with nesting vireos, current threats, and proposed steps that might be needed for their rebound in numbers.

List of equipment required: A vehicle to travel to different sites, a physical or digital fieldbook, a handheld GPS unit, trail cameras, and binoculars.

5. Increased public awareness on Bermuda vireo breeding behavior, nesting threats, and habitat management.

Actions proposed:

- Research lectures on the breeding biology and threats faced by Bermuda vireos,
- Create a “Backyard Vireo Management” pamphlet for public dissemination,
- Make these pamphlets available for landowners with small (i.e., at least 0.5 - 1 ha) and large (≥ 1 ha) woodlands,
- Advocate that landowners attempt to do extensive tree removal outside the Bermuda vireo nesting season, to prevent breeding disruptions,
- Similarly, suggest to landowners interested in native forest restoration to do a gradual cull and replant approach, as opposed to total eradication of invasive trees and replanting young, native trees.

Work Team: DENR and MM

Team Leader(s): MM and DENR

Assistance: BAMZ, BZS, BAS, general public, landowners, hired groundskeepers of managed sites.

Outputs: Increased island-wide awareness of the reliance of Bermuda vireos on their wooded habitat, and how subtle changes to landscaping practices may benefit this subspecies.

List of equipment required: A vehicle to travel to different sites, landscaping equipment that is appropriate for targeted trees, and binoculars.

F. Estimated Date of Down Listing

The Bermuda White-eyed Vireo is currently listed as ‘Vulnerable’ (D1 + 2) under the Protected Species Amendment Order (2016). Despite its present-day island-wide distribution in nearly all thickets and woodlands, an official estimate of their numbers is currently unknown. The suggested series of capture, ringing, and monitoring programs in this Management Plan is essential in obtaining a more accurate estimate of their abundance, so that strategic decisions can be made with respect to down listing. Their island-wide distribution, high mist nest catchability, and tameness, are all traits that favour feasible assessment of their survival and abundance in the wild. A population assessment study of at least 5 years should be sufficient to determine a reliable estimate of population size and health necessary to consider the Bermuda vireo as a suitable candidate for down listing.

PART III: IMPLEMENTATION

Priority 1: An action that must be taken to prevent extinction or to prevent the species from declining irreversibly.

Priority 2: An action that must be taken to prevent a significant decline in the species population/habitat quality, or some other significant negative impact short of extinction.

Priority 3: All other action necessary to provide for full recovery of the species.

Priority #	Task #	Task description	Task Duration	Responsible Party
		Population Size and Survival		
2	1	mist netting vireos	ongoing	MM
2	2	revisiting field sites	ongoing	MM
2	3	mapping general study sites	1-2 months	MM
3	17	encourage public bird sightings	ongoing	MM, DENR, BAS
		Territory Mapping		
2	4	collect GPS points	ongoing	MM
2	5	map GPS points	1 year	MM
2	6	monitor breeding of ringed vireos	ongoing	MM
		Nest predator control		
2	7	lecture to public	ongoing	MM, BAS
2	8	presence and abundance surveys	1-4 days	MM, DENR, BAS
2	9	promote nest predator control	ongoing	MM, DENR, BAS
2	10	work plan with BVC	1-2 days	MM, DENR, BAS
2	11	post-predation control follow-up	1-2 days	MM
2	12	monitor fledglings heard	4-5 months	MM, DENR, BAS
		Silk Spider Surveys		
3	18	encourage public to report sightings	1-2 years	MM, DENR, BAMZ
3	19	field surveys on spiders	1-2 years	MM, DENR, BAMZ
3	20	assess field observations and cameras	2 years	MM, DENR, BAMZ
		Public Awareness and Management		
2	13	public lectures	ongoing	MM, BAS, DENR
2	14	promote alternate tree culling strategies	ongoing	MM, BAS, DENR
2	15	create vireo management pamphlet	2-3 weeks	MM, DENR
2	16	make pamphlet available to public	4-5 months	MM, DENR

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