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

Miguel Mejias[1] and David Wilson[1]

[1]Memorial University of Newfoundland

December 14, 2022

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. Furthermore, male songbirds may adjust when and where they sing throughout the breeding season, depending on their breeding stage. However, such relationships remain untested in several avian taxa. Here, we 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. We compare song rate and song perch height among different stages of the breeding season and during the non-breeding season. We show that male vireos produce both song types during the breeding and non-breeding seasons, suggesting dual roles in mate choice and territorial defence. 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 versus rambling songs. Our findings suggest that male vireos 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, our 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.

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

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. Furthermore, male songbirds may adjust when and where they sing throughout the breeding season, depending on their breeding stage. However, such relationships remain untested in several avian taxa. Here, we 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. We compare song rate and song perch height among different stages of the breeding season and during the non-breeding season. We show that male vireos produce both song types during the breeding and non-breeding seasons, suggesting dual roles in mate choice and territorial defence. 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 versus rambling songs. Our findings suggest that male vireos 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, our 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.

Keywords: Bermuda White-eyed Vireo, breeding behaviour, daytime singing, island songbirds, song perch selection, vireos,

Introduction

Bird song is diverse among species, yet also varies within species (Mejías et al. 2020, Rose et al. 2022). One hypothesis for explaining 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 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 songs of the same species.

Several hypotheses exist to explain variation in singing behaviour and its effects on conspecific receivers. For example, during the breeding season, male Great Tits (*Parus major*) that are removed from their territories and replaced with speakers broadcasting their song experience fewer territorial intrusions than controls that are removed and replaced with speakers broadcasting silence (Krebs 1977). This finding provides 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 is highest during nestling care (Morton et al. 1993, Burhans et al. 2002). The cost of nest failure may also increase during 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, such as 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 are related to 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. Only males sing, and their songs are described as fast and robotic in delivery (Adkission and Conner 1978, Borror 1987). Two distinctive song types are recognized, discrete song and rambling song (Bradley 1980). The discrete song type 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 type 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 interactions with females (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 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, we 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, to investigate the mate attraction and nest predation hypotheses, we test whether vocal output is associated with a male's nesting status within the breeding season. We 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, we 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), we 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 that are thought to function in female attraction rather than discrete songs that are thought to function in territory defence (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, approximately 1048 km from its closest landmass, Cape Hatteras, North Carolina. 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). We collected data at Spittal Pond Nature Reserve (60 acres) and Ferry Reach Park (64 acres) (Figure 1). Present-day wooded habitat in Bermuda is dominated by invasive secondary forest (Mejías and Nol 2020, Mejías and Mejías 2020). Trees in our study sites included introduced Brazilian pepper (*Schinus terebinthifolius*), casuarina (*Casuarina equisetifolia*), and fiddlewood (*Citharexylum spinosum*), and a few native trees including southern hackberry (*Celtis laevigata*), bay grape (*Coccoloba uvifera*), and Bermuda cedar (*Juniperus bermudiana*).

In May 2018, January 2019, and April 2019, we captured 10 male vireos and 4 female vireos. Birds were captured along walking trails at Spittal Pond and Ferry Reach Park by luring them into mist nests with playback of conspecific song. We 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 playbacks was weak and we were unable to capture the remaining females associated with captured males. We fitted captured birds with an aluminum Porzana identification band on one leg and either one or two plastic colour bands on the other leg. We released banded birds at their point of capture within 10 min. To increase our sample size, we also included 4 previously colour-banded vireos (2 males and 2 females) living at Ferry Point Park. In total, we had 12 colour-banded males that served as our

focal subjects (Spittal Pond: 7 males; Ferry Point Park: 5 males). All 6 colour-banded females were mates to focal males.

Throughout the data collection periods of the breeding season (April 2019– August 2019) and the non-breeding season (December 2019– January 2020) , we estimated territorial boundaries by opportunistically following each subject for 1– 2 hours per day on several days and taking GPS coordinates of used perches. We 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). In general, territories birds were captured in during the 2018– 2019 banding period were the same as during the 2019– 2020 data collection period. Two exceptions occurred: (1) one male we captured in January 2019, for which we had yet to map his original territory, had, by April 2019, taken over a territory previously occupied by another colour-banded male, independent of our study, approximately 100 m away, and (2) a male we banded in December 2018 was present for the entire breeding season study had disappeared by December 2019, thus reducing our sample to 11 males for analyses involving the non-breeding season.

Singing behaviour

Our general approach was to monitor male Bermuda Vireos intensively over a prolonged period to observe changes in their singing behaviour across multiple breeding stages of the breeding season as well as during the non-breeding season. We audio-recorded the daytime (0700–1200 h) singing behaviour of the 12 male birds throughout most of the subspecies' breeding season (April 2019 – August 2019). Of these 12 males, 11 were relocated and recorded during a brief period of the following non-breeding season (December 2019 – January 2020). Researchers often record birds at or just before dawn (Bolsinger 2000, Dolan et al. 2007, MacDonald and Islam 2021) when passerine song typically peaks (Staicer et al. 1996, Dabelsteen and Mathevon 2002). We 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 our sampling regime, we visited one of our two sites each day during favorable weather (i.e., no rain and little to no wind), alternating between sites each day. In total, we visited the Ferry Reach Park site 41 times during the breeding season and 5 times during the nonbreeding season. We visited the Spittal Pond site 44 times during the breeding season and 7 times during the nonbreeding season. While at a site, we recorded each male at the site during a separate 15-minute recording session throughout the morning. Our goal was to obtain unbiased estimates of singing behaviour from each male across multiple breeding stages. We therefore randomized the order in which we 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, we searched for him for [?] 15 min. If we found him, we waited 2 min before commencing recording. The 2-min delay was important because we sometimes located subjects by hearing them sing. Since our goal was to obtain unbiased estimates of singing behaviour, including estimates of daily song production, waiting for 2 min reduced the risk of biasing our recording sessions towards periods of time when the male was known to be singing. If we did not see or hear the focal male after 15 min, we 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 our familiarity with the song repertoires of the 12 birds, we were confident that we 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 his territory, we immediately approached him while recording. If we located the singing male and confirmed that he was our focal subject, we included in our 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 we located was not the focal subject (e.g., a neighbour), we aborted the recording session and repeated it later that day.

We 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 no closer than 5 m while pointing the microphone directly at him (or towards the source of the songs if we had not yet located him). For each song produced while the subject was visible, we spoke into the microphone and visually estimated his song perch height above the ground (estimated accuracy +- 1 m); very few trees across Bermuda Vireo territories were > 10 m; all height estimates were made by the same person. We noted any periods in which we lost visual contact with the subject, but always continued recording until the 15-min session expired. After recording, if confirmed visually, we used a handheld GPS unit (Garmin eTrex(r) 0, ~3 m accuracy; Garmin International, Inc., Olathe, KS, USA) to mark general singing localities (separated by [?] 5 m) of each male, per trial. We used [?] 5 m because Bermuda Vireos move continuously through their territories with short (~0.3 - 1.0 m) flutter hops interspersed occasionally by longer (up to a few metres) loping flights (M. Mejias pers. observations).

In May 2021, we returned to our sites and measured the heights of the two tallest trees in each subject's territory to allow comparisons between the heights of the song perches used by our subjects during recording and the heights of the tallest perches available to our subjects. We 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 +- 1m) any 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 (April 2019 – August 2019), we revisited subjects in the afternoons (1300–1700 h) to document their breeding activities. We spent a maximum of 30 min searching for a given male, and usually found them on account of their loud vocalizations and small territories. We 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; Mejias 2021). We defined nest building as the stage when vireos are adding materials to a nesting branch until a nest is completed. We defined the egg stage as the period after nest completion, when the vireos are engaged in egg laying and incubation; the egg stage 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 we were 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 occurs in our study system. For example, one of our 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 we were unable to find her and that they had remained paired throughout. To avoid the ambiguity of assigning paired and unpaired status, we instead categorized males as with or without "nesting duties." During the breeding season, we 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 not engaged in any of the above nesting behaviours with a female. We often could not see a female accompanying a male that was without nesting duties, but we 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 (Mejias et al. 2021). For this reason, some of the focal males experienced the same

nesting stage multiple times throughout the breeding season. Whenever possible, we 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 (Mejias 2021). Predation from ants was obvious because swarms would usually 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, we recorded its location with the same GPS unit. We 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

We generated a waveform and spectrogram (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, we 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. We 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 (Mejias et al. 2020, Mejias et al. 2021). Our song definition did not hinder our ability to identify discrete songs and rambling songs (Figure 2), as defined by Bradley (1980: Figures 1B, 2A, B, and C). In total, we annotated 17,682 vireo songs from 430 15-min recordings. To make our 15-min measure of vocal activity comparable to previous studies, we multiplied the number of discrete and rambling songs in each recording session by four to obtain hourly rates.

Statistical analyses

Statistical analyses were conducted using R (3.5.2; R Development Core Team, R Foundation of Statistical Computing, Vienna, Austria). In our first analysis, we used a generalized linear mixed model (*lme4* package; Bates et al. 2015) to test whether the number of discrete songs per hour varied among the six breeding stages. We 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). We 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.

In our second analysis, we used a generalized linear mixed model to test whether song perch height was associated with breeding stage or song type. 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 $P < 0.05$. We 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. We 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, we 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 we observed this at both the edge and interior of a singer's territory. Our fieldwork produced 430 15-min recordings across the breeding (April 2019–August 2019; $N = 374$ recordings) and non-breeding seasons (December 2019–January 2020; 56 recordings), equating to 6,450 min. We obtained more recordings of focal males during the breeding season (mean +- 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 males) because our winter residency on the island was limited compared to the summer months, and because the breeding season was subdivided into five stages. 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 3). We noted that August also marked the onset of feather moult in our 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 +- 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 and predation rates

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, we found 34 completed nests across the 12 focal territories. We found nest predation to be highest during the nestling care stage. More specifically, we recorded 10 predation events, of which 9 (26%) were of known stages: 2 (6%) during the egg stage and 7 (21%) during nestling care. We found the 10th attacked by Argentine ants, which only attack nests with edible contents, the day after its discovery, before we could confirm weather eggs or nestlings were inside. Therefore, it is unclear whether it had been predated during late-egg stage or early nestling stage.

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 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 $\pm$ 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 $\pm$ 0.81; Z = 3.46, $P = 0.0005$). Discrete song rate also was lower during nestling care

than during other nesting stages (mean of nest building, incubation, and fledgling care; estimate $\pm$ SE (log scale): -2.87 $\pm$ 0.99; Z = 2.89, P = 0.0039).

Factors associated with song perch height

We estimated song perch heights for 6,793 of the 17,682 (34%) songs recorded. Males sang from a wide range of perch heights (5 $\pm$ 3 m; 1–17 m; Table 1, Figure S1), but rarely sang from the tallest available perches (15 $\pm$ 4 m; 9–22 m; Table 1). Song perch height varied significantly among the six breeding stages (Analysis of Deviance: χ^2 = 25.05, df = 5, P = 0.0001) and between the two song types (χ^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 $\pm$ 0.50; Z = 2.27, P = 0.0235; Figure 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 $\pm$ 0.27; Z = 3.25, P = 0.0012; Figure 5B). Song perch height also differed significantly between rambling and discrete songs (χ^2 = 8.01, df = 1, P = 0.0047), with males singing rambling songs from significantly lower perches (estimate $\pm$ SE (log scale): -0.11 $\pm$ 0.04; Z = -2.83, P = 0.0047; Figure 5C.).

Discussion

The singing behaviour of territorial male Bermuda Vireos was related to their breeding activities. Although the Bermuda Vireo can be heard year-round, our study suggests that males become 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 used discrete songs more extensively than rambling songs year-round, and discrete song rate did not differ between the breeding and non-breeding seasons. During the breeding season, however, 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 (Lawrence 1953; Graber 1961; Nolan 1960; Nolan 1962; James 1978; Bradley 1980; Robinson 1981; Gomez-Montes and Moreno 2008; Hedley 2016); for *V. griesus*, the former and latter song types are known as "discrete songs" and "rambling songs," respectively. 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 territory 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 (Bradley 1981), and we were unable to compare its rate of production between seasons. Nevertheless, several observations support a territorial defence function for rambling song. It is produced in the non-breeding season and, compared to discrete songs, is produced lower in the canopy, where male-male interactions typically occur (Liu 2004). Although anecdotal, Bermuda Vireos in our study sang rambling songs during several close-quarter countersigning exchanges with neighbouring males. We note, however, that one male also directed rambling song towards a female moments before copulating with her, suggesting that rambling songs might also function in a breeding context.

Our findings also 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 time singing discrete songs at a high rate, whereas males with nesting duties were most often accompanied by a female and sang significantly fewer discrete songs. 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). Our 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 discrete song functions to

8

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, Liu and Kroodsma 2007); these researchers suggest that singing from elevated perches increases an unmated male's visual and acoustic 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 following nest failure. The tendency of males to select higher perches when singing discrete song versus rambling song might be because discrete song is louder than rambling song (Bradley 1980); the combination of being louder and being sung from higher perches may reflect a history of selection for maximizing signal transmission distance (Sprau et al. 2012, Podos and Sung 2020).

Most of the nest predation in our 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 familes, 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). Our observation of song resurgence during the fledgling stage (Figure 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. 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. obvs.), when 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 stages in birds (Rohwer et al. 2009, Kulaszewicz and Jakubas, 2015), and could also explain the 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, we found that male Bermuda Vireos are year-round singers that alter their singing behaviour in relation to breeding stage. Our 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 during nestling care when their nests are at the greatest risk of predation.

Literature Cited

Adkisson C. S. and R. N. Conner. 1978. Interspecific vocal imitation in White-eyed Vireos. The Auk 95: 602–606.

Amos, E. 1991. A guide to the birds of Bermuda. Warwick, Bermuda.

Bangs, O. and T. S. Bradley. 1901. The resident land birds of Bermuda. The Auk 18: 249–257.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Barker, N. K. and D. J. Mennill. 2009. Song perch height in Rufous-and-White Wrens: does behaviour enhance effective communication in a tropical forest? Ethology 115: 897–904.

Beck, M. J. and T. L. George. 2000. Song post and foraging site characteristics of breeding Varied Thrushes in northwestern California. The Condor 102: 93–103.

Bolsinger, J. S. 2000. Use of two song categories by Golden-cheeked Warblers. The Condor 102: 539–552.

Borror, D. J. 1987. Song in the White-eyed Vireo. The Wilson Bulletin 99: 377–397.

Bradley, R. A. 1980. Vocal and territorial behavior in the White-eyed Vireo. The Wilson Bulletin 92: 302-311.

Bradley, R. A. 1981. Song variation within a population of White-eyed Vireos (Vireo griseus). The Auk, 98: 80–87.

Brunner, P. and Pasinelli, G. 2010. Variation in singing style use in the reed bunting *Emberiza schoeniclus* : influencing factors and possible functions. Journal of Avian Biology 41: 388–397.

Burhans, D. E., D. Dearborn, F. R. Thompson III, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. Journal of Wildlife Management 66: 240–249.

Campos, D. P., L. A. Bander, A. Raksi, and D. T. Blumstein. 2009. Perch exposure and predation risk: a comparative study in passerines. Acta Ethologica 12: 93.

Castrale, J. S. 1983. Selection of song perches by sagebrush-grassland birds. The Wilson Bulletin 95: 647–655.

Catchpole, C. K. and Slater, P. J. 2003. Bird song: biological themes and variations. Cambridge University Press.

Chiver, I., E. S. Morton, and B. J. Stutchbury . 2007. Incubation delays territory defense by male blue-headed vireos, *Vireo solitarius* . Animal Behavior 73: 143–148.

Dabelsteen, T. and N. Mathevon. 2002. Why do songbirds sing intensively at dawn? Acta Ethologica 4: 65–72.

Demko, A. D., L. R. Reitsma, and C. A. Staicer. 2013. Two song categories in the Canada Warbler (*Cardellina canadensis*). The Auk 130: 609–616.

Dolan, A., K. Sexton, L. Redmond, and M. Murphy . 2007. Dawn song of Eastern Kingbirds: intrapopulation variability and sociobiological correlates. Behaviour 144: 1273–1295.

Duncan, W. J. and P. A. Bednekoff. 2006. Singing in the shade: song and song posts of Northern Cardinals near nesting Cooper's hawks. Canadian Journal of Zoology 84: 916–919.

Ellison, A. M. and R. Ydenberg. 2019. Risk allocation: acute and chronic predator exposure have contrasting effects on Song Sparrow (*Melospiza melodia*) singing behaviour. Canadian Journal of Zoology 97: 258–266.

Ficken, M. S. and R. W. Ficken. 1962. The comparative ethology of the wood warblers: A review. Living Bird 1: 103–122.

Foote, J. R., L. P. Fitzsimmons, L. M. Lobert, L. M. Ratcliffe, and D. J. Mennill . 2017. A population-level analysis of morning song: exploring the implications for point counts. Canadian Field-Naturalist 131: 10–18.

Fox, J. and S. Weisberg . 2019. An R Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. URL: https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gomez-Montes, C., and M. I. Moreno. 2008. Breeding phenology and nesting habitat characterisation of the San Andres Vireo (*Vireo caribaeus*). Bird Conservation International 18: 319–330.

Graber, J. W. 1961. Distribution, habitat requirements, and life history of the Black-capped Vireo (*Vireo atricapilla*). Ecological Monographs 31: 313–336.

Greig-Smith, P. W. 1983. Use of perches as vantage points during foraging by male and female Stonechats *Saxicola torquata* . Behaviour 86: 215–236.

Guilfoyle, M. P., R. A. Fischer, and J. S. Wakeley. 2002. Perch characteristics of Acadian Flycatchers (*Empidonax virescens*) in southern bottomland hardwood forests. Southeastern Naturalist 1: 353–364.

Haff, T. M., A. G. Horn, M. L. Leonard, and R. D. Magrath.2015. Conspicuous calling near cryptic nests: a review of hypotheses and a field study on white-browed scrubwrens Journal of Avian Biology 46: 289–302.

Hallworth, M., A. Ueland, E. Anderson, J. D. Lambert, and L. Reitsma. 2008. Habitat selection and site fidelity of Canada Warblers (*Wilsonia canadensis*) in central New Hampshire. The Auk 125: 880–888.

Hartig, F. 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.3.3.0.*http://florianhartig.github.io/DHARMa/*.

Hayes, J. P., J. R. Probst, and D. Rakstad. 1986. Effect of mating status and time of day on Kirtland's Warbler song rates. The Condor 88: 386–388.

Hedley, R. W. 2016. Composition and sequential organization of song repertoires in Cassin's Vireo (*Vireo cassinii*). Journal of Ornithology. 157: 13–22.

Howes-Jones, D. 1985. Relationships among song activity, context, and social behavior in the Warbling Vireo. The Wilson Bulletin 97: 4–20.

James, R. D. 1978. Pairing and nest site selection in Solitary and Yellow-throated vireos with a description of a ritualized nest building display. Canadian Journal of Zoology 56: 1163–1169.

James, R. D. 1984. Structure, frequency of usage, and apparent learning in the primary song of the Yellow-throated Vireo, with comparative notes on Solitary Vireos (Aves: Vireonidae). Canadian Journal of Zoology 62: 468–472.

James, R. D. 1999. Yellow-throated and Blue-headed Vireos in Ontario: 5. Nestling period, and post-nesting activities. Ontario Birds 17: 14–21.

Janes, S. W., L. Ryker, and R. M. Ryan. 2017. Yellow-rumped Warblers use two song categories: each male tends to use a unique song in each category in Southern Oregon. Northwestern Naturalist 98: 1–7.

Krebs, J. R. 1977. Song and territory in the great tit. Pages 47-62 in: Evolutionary ecology (Stonehouse B, Perrins CM, Eds), Macmillan, London.

Kroodsma, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. The Auk 101: 13–24.

Kulaszewicz I. and D. Jakubas. 2015. Factors affecting post-breeding moult in the Savi's Warbler *Locustella luscinioides*in northern Poland. Ardea. 103: 61–68.

Lawrence, L. D. K. 1953. Nesting life and behavior of the Red-eyed Vireo. Canadian Field-Naturalist 67: 47–77.

Liu, W. C. 2004. The effect of neighbours and females on dawn and daytime singing behaviours by male Chipping Sparrows. Animal Behavior 68: 39–44.

Liu, W. C. and D. E. Kroodsma. 2007. Dawn and daytime singing behavior of chipping sparrows (*Spizella passerina*). The Auk 124: 44–52.

Lenth R. V. 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.4. https://CRAN.R-project.org/package=emmeans

MacDonald, G. J. and K. Islam. 2021. Do social factors explain seasonal variation in dawn song characteristics of paired male Cerulean Warblers (*Setophaga cerulea*)? Bioacoustics 30: 1–16.

Mathevon, N., T. Dabelsteen, and S. H. Blumenrath. 2005. Are high perches in the Blackcap *Sylvia atricapilla* song or listening posts? A sound transmission study. Journal of the Acoustical Society of America 117: 442–449.

McDonald, P. G., D. R. Wilson, and C. S. Evans. 2009. Nestling begging increases predation risk, regardless of spectral characteristics or avian mobbing. Behavioral Ecology 20: 821–829.

Mejias, M. A. 2021. Management Plan for the Bermuda White-eyed Vireo (*Vireo griseus bermudianus*). Department of Environment and Natural Resources, Government of Bermuda. 1–36.*https://environment.bm/species-recovery-plans.*

Mejias, M. A. and A. J. Mejias. 2020. Mass fallout and stopover duration of migratory Blackpoll Warblers (*Setophaga striata*) in Bermuda after Hurricane Nicole. Journal of Caribbean Ornithology 33: 15–21.

Mejias, M. A. and E. Nol . 2020. Woodland size and vegetation effects on resident and non-resident woodland birds in Bermuda. Journal of Caribbean Ornithology 33: 22–32.

Mejias, 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.

Mejias, M. A., J. Roncal, and D. R. Wilson. 2021. Territorial responses of male Bermuda White-eyed Vireos (*Vireo griseus subsp. bermudianus*) reflect phylogenetic similarity of intruders and acoustic similarity of their songs. Journal of Field Ornithology 92: 431–449.

Mennill, D., T. Dabelsteen, and N. Barker. 2009. Degradation of male and female Rufous-and-white Wren songs in a tropical forest: effects of sex, perch height, and habitat. Behaviour 146: 1093–1122.

Moran, I. G., K. C. Lukianchuk, S. Doucet, A. E. Newman, H. Williams, D. R. Norris, and D. J. Mennill. 2019. Diel and seasonal patterns of variation in the singing behaviour of Savannah Sparrows (*Passerculus sandwichensis*). Avian Research 10: 1–8.

Morton, M. L., K. W. Sockman, and L. E. Peterson. 1993. Nest predation in the Mountain White-crowned Sparrow. Condor 95: 72–82.

Nice, M. M. 1930. A study of a nesting of Black-throated Blue Warblers. The Auk 47: 338–345.

Nolan, V. 1960. Breeding behavior of the Bell Vireo in southern Indiana. The Condor 62: 225–244.

Nolan, V. 1962. The swaying display of the Red-eyed and other vireos. The Condor 64: 273–276.

Nowicki, S., S. Peters, and J. Podos. 1998. Song learning, early nutrition and sexual selection in songbirds. American Zoologist 38: 179–190.

Petit, K. E., D. R. Petit, and L. J. Petit. 1988. On measuring vegetation characteristics of bird territories: nest sites vs. perch sites and the effect of plot size. The American Midland Naturalist 119:

209–215.Podos, J. and H. C. Sung. 2020. Vocal performance in songbirds: From mechanisms to evolution. In The neuroethology of birdsong (pp. 245-268). Springer, Cham.

Podos, J. and H. C. Sung. 2020. Vocal performance in songbirds: From mechanisms to evolution. In The neuroethology of birdsong (pp. 245-268). Springer, Cham.

Powlesland, R. G. 1983. Seasonal and diurnal variation in vocal behaviour of the South Island Robin. New Zealand Journal of Ornithology 10: 225–232.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

Robinson, S. K. 1981. Ecological relations and social interactions of Philadelphia and Red-eyed vireos. The Condor 83: 16–26.

Rodenhouse, N. L. and L. B. Best. 1983. Breeding ecology of vesper sparrows in corn and soybean fields. American Midland Naturalist 110: 265–275.

Rohwer, V. G., S. Rohwer, and M. F. Ortiz-Ramirez. 2009. Molt biology of resident and migrant birds of the monsoon region of west Mexico. Ornitologia Neotropical 20: 565–584.

Rose, E. M., N. H. Prior, and G. F. Ball. 2022. The singing question: re-conceptualizing birdsong. Biological Reviews 97: 326-342.

Slagsvold, T. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. Journal of Animal Ecology 53: 945–953.

Sockman, K. W., K. B. Sewall, G. F. Ball, and T. P. Hahn. 2005. Economy of mate attraction in the Cassin's Finch. Biology Letters 1: 34–37.

Sprau, P., T. Roth, M. Naguib, and V. Amrhein. 2012. Communication in the third dimension: song perch height of rivals affects singing response in nightingales. PLoS One 7: e32194.

Spector, D. A. 1991. The singing behaviour of Yellow Warblers. Behaviour 117: 29–52.

Spector, D. A. 1992. Wood-warbler song systems. A review of paruline singing behaviors. In: Current ornithology, vol. 9. D. M. Power, ed. Boston (MA): Springer US; p. 199–238.

Staicer, C. A. 1989. Characteristics, use, and significance of two singing behaviors in Grace's Warbler (*Dendroica graciae*). The Auk 106: 49–63.

Staicer, C.A., D. A. Spector, and A. G. Horn. 1996. The dawn chorus and other diel patterns in acoustic signaling. In: Ecology and evolution of acoustic communication in birds. Kroodsma, D. E., Miller, E. H., eds. Cornell University Press, Ithaca, NY pp 426–453.

Staicer, C. A., V. Ingalls, and T. W. Sherry. 2006. Singing behavior varies with breeding status of American Redstarts (*Setophaga ruticilla*). The Wilson Journal of Ornithology 118: 439–451.

Szymkowiak, J. and L. Kuczyński. 2017. Song rate as a signal of male aggressiveness during territorial contests in the wood warbler. Journal of Avian Biology 48: 275–283.

Tobias, J. A., C. Sheard, N. Seddon, A. Meade, A. J. Cotton, and S. Nakagawa. 2016. Territoriality, social bonds, and the evolution of communal signaling in birds. Frontiers in Ecology and Evolution 4: 74.

Verhulst, S. and J. A. Nilsson. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society B 363: 399–410.

Verrill, A. E. 1902. The Bermuda Islands. An Account of their Scenery, Climate, Productions, Physiography, Natural History and Geology, with Sketches of their Discovery and Early History, and the Changes in

their Flora and Fauna Due to Man. Transactions of the Connecticut Academy of Arts and Scienc-es, Vol. XI, Part II. Connecticut Academy of Arts and Sciences, New Haven, CT.

Wheeldon, A., P. Szymański, and T. S. Osiejuk. 2021. Yellow-breasted Boubous (*Laniarius atroflavus*) jointly defend territories with male-led duets against stranger pairs, males and females. Ethology 127: 176–186.

Wilson, D. M. and J. Bart. 1985. Reliability of singing bird surveys: effects of song phenology during the breeding season. The Condor 87: 69–73.

Table 1. Heights 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, the sample size, and 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 2
BlackWhiteBlue	4 $\pm$ 0.46; 4–5; 8	3 $\pm$ 0.74; 3–5; 8	4 $\pm$ 2.77; 1–12; 133	15^{CA}; 20^{C}
BlueBluePink	4 $\pm$ 1.17; 2–6; 68	5 $\pm$ 2.68; 1–14; 368	4 $\pm$ 1.35; 2–6; 96	13^{CA}; 15^{C}
BlueGreen	NA	5 $\pm$ 1.79; 1–7; 168	4 $\pm$ 1.72; 1–8; 126	16^{CA}; 18^{C}
BlueRed	2 $\pm$ 0.84; 1–3; 5	6 $\pm$ 2.10; 2–9; 63	5 $\pm$ 1.99; 1–8; 597	**10^{SH};14^{F}**
GreenOrange	5 $\pm$ 0.91; 2–7; 121	5 $\pm$ 0.93; 2–7; 130	5 $\pm$ 1.61; 1–8; 396	9^{FW};11^{CA}
GreenRed	3 $\pm$ 1.25; 1–5; 43	4 $\pm$ 3.71; 1–14; 331	5 $\pm$ 2.35; 1–10; 405	18^{C}; 21^{C}
OrangePurple	4 $\pm$ 1.60; 1–6; 42	2 $\pm$ 1.41; 1–5; 56	4 $\pm$ 2.36; 1–10; 380	14^{C}; 15^{C}
Pink	2 $\pm$ 0.71; 1–3; 8	4 $\pm$ 1.32; 1–5; 246	3 $\pm$ 1.23; 1–6; 118	11^{IL}13^{C}
Purple*	NA	4 $\pm$ 1.87; 1–8; 199	5 $\pm$ 3.63; 1–14; 65	10^{FW};10^{F}
RedPink	3 $\pm$1.36; 1–6; 88	8 $\pm$ 4.36; 1–17; 1285	4 $\pm$ 2.27; 1–12; 128	17^{C}; 18^{C}
WhiteGreen	NA	9 $\pm$ 2.90; 1–14; 701	5 $\pm$ 1.69; 1–8; 162	13^{C}; 15^{C}
YellowBlue	2 $\pm$ 1.40; 1–8; 66	3 $\pm$ 1.63; 1–12; 46	4 $\pm$ 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).
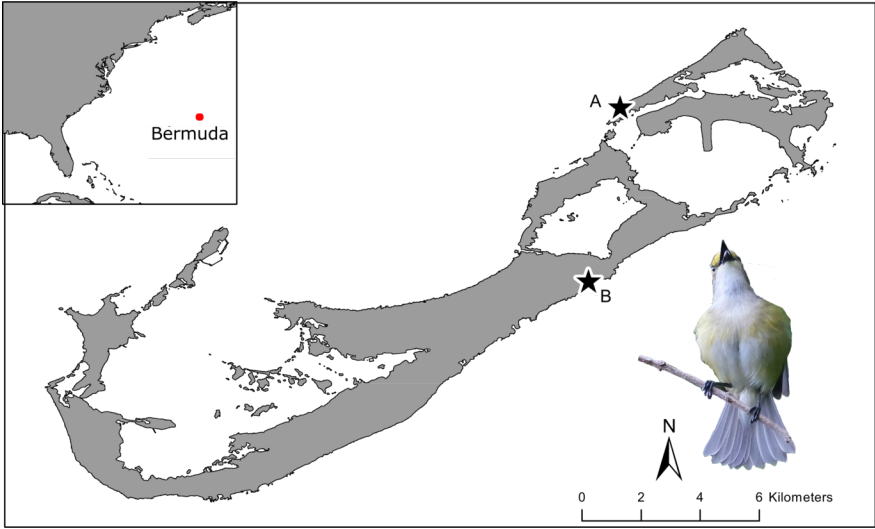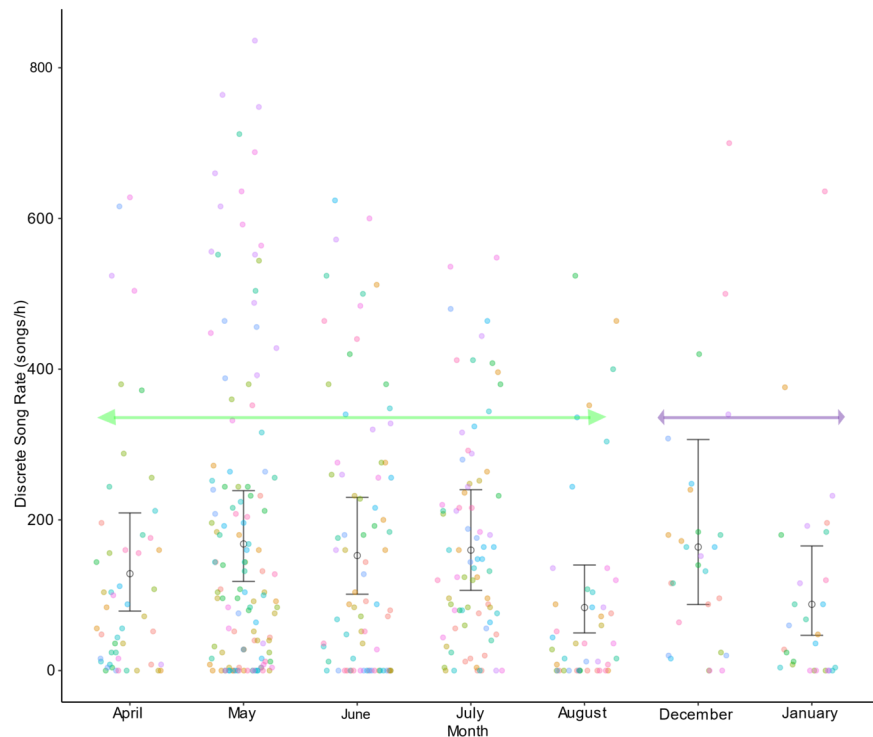
Figures

Figure 1. Two sites in Bermuda where 12 colour-banded male Bermuda 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.
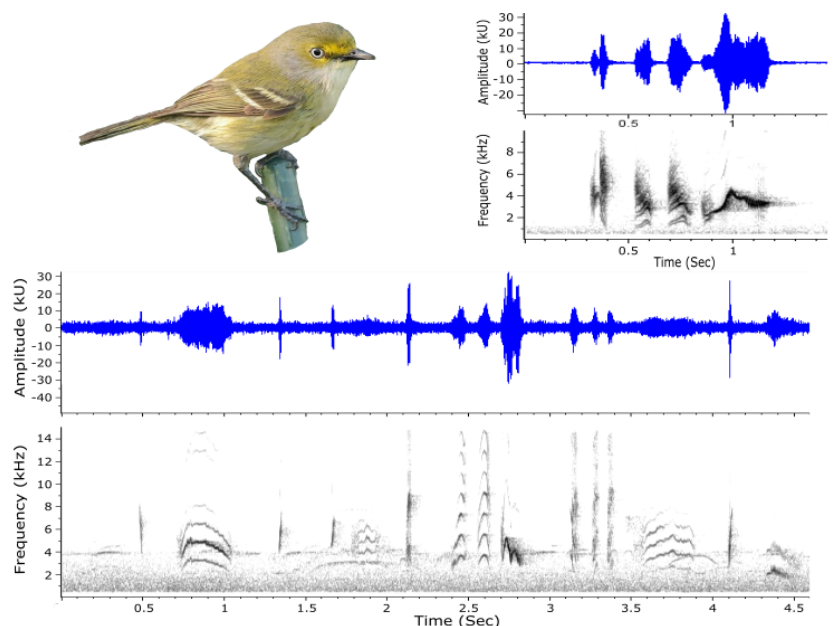

Figure 2. Waveforms and spectrograms depicting the two song types of male Bermuda Vireos: discrete song (top right panels) and rambling song (bottom panels). The discrete song is short (ca. 1 s) and comprises highly modulated elements, including chips, buzzes, and whistles delivered in a fixed sequence; males repeat the same sequence several times before switching to another distinct discrete song variant 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. Frequency is shown in kilohertz (kHz), amplitude in kilounits (kU; these are the digitized sample values in the signal and are proportional to the sound pressure at the microphone during recording), and time in seconds (Sec). Photograph by Richard Brewer.

Figure 3. Discrete song rate (songs/h) of male Bermuda 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 (discrete song rate was included as the dependent variable, with month as a fixed factor, and subject identity (1–12) as a random effect) with a negative binomial distribution 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.
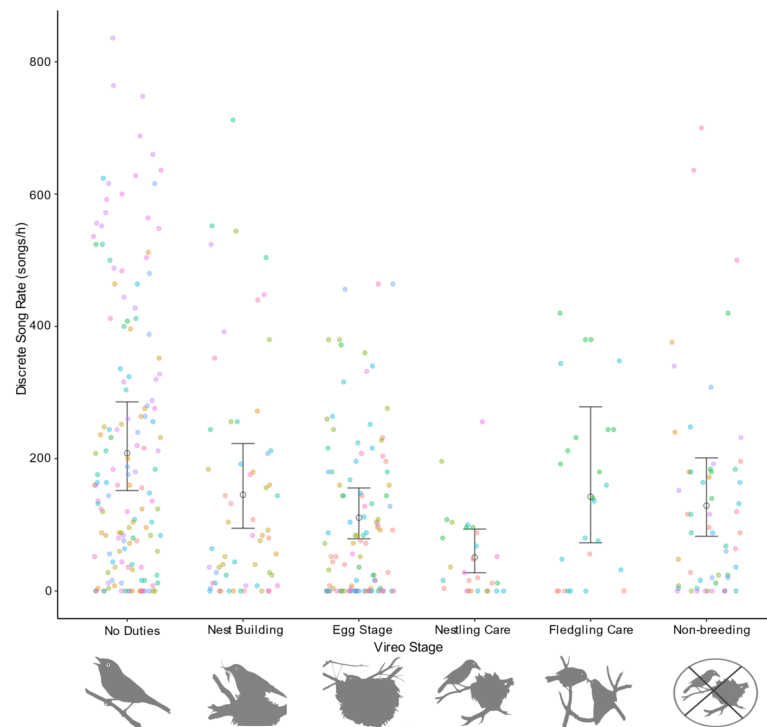
Figure 4. Discrete song rate (songs/h) of male Bermuda Vireos across six breeding stages: (1) no nesting duties, (2) nest building, (3) egg stage, (4) nestling care, (5) fledgling care, and (6) non-breeding. Estimated marginal means and 95% confidence intervals derived from a generalized linear mixed 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.
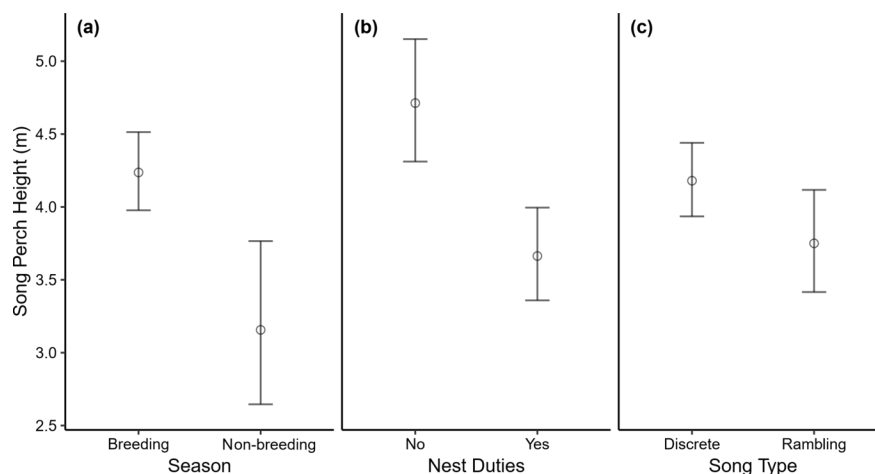
Figure 5. Song perches of male Bermuda Vireos were higher (a) in the breeding season than in the non-breeding seasons, (b) among males with no nesting duties than among males with nesting duties during the breeding season, and (c) when males sang discrete songs versus rambling songs. Estimated marginal

17

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.