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Research article

The relationships of breeding stage to daytime singing behaviour and song perch height in Bermuda white-eyed vireos *Vireo griseus bermudianus*

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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 and territory defence hypotheses. We compare song production 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. Song production did not differ significantly between the breeding and non-breeding seasons, but, within the breeding season, males without nesting duties sang significantly more songs than males with nesting duties. 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 song production 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.

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

Introduction

Bird song varies widely among species, but also within species and within individuals (Catchpole and Slater 2003, Mejías et al. 2020, Rose et al. 2022). Birds sing from

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different locations, including on the ground (Leston et al. 2015), in dense tree cover (Cibois et al. 2019), on open, elevated perches (Jones and Islam 2006), and even while in flight (Thompson et al. 2020). Temporal components of song also vary. Song rate, for example, varies seasonally and throughout the day (Avey et al. 2011, Odom et al. 2016, Fahmy and Wilson 2020), and these patterns can differ for migratory species that sing primarily on their temperate breeding grounds (Emlen 1973) and Neotropical species that sing year-round (Demko and Mennill 2018). Although song research has traditionally focused on males (Rose et al. 2022), female song is prevalent in many species and is likely the ancestral state (Riebel et al. 2019). With respect to song structure, structurally distinct song types can serve different functions. In New World warblers (Parulidae), the males of some species reserve structurally complex songs for male–male interactions and simpler songs with more stereotyped structure for interactions with females (Ficken and Ficken 1962, Staicer 1989, Janes et al. 2017). In other species, such as white-crowned sparrows *Zonotrichia leucophrys pugetensis* (Nelson and Poesel 2011) and black-capped chickadees *Poecile atricapillus* (Otter and Ratcliffe 1993), males use a single song type during interactions with both sexes. Considering the broad variation in singing behaviour and song structure, testing hypotheses about when and where songbirds sing can provide insight into the function of avian song (Catchpole and Slater 2003, Mejías et al. 2020, Rose et al. 2022). In the current study, we focus on whether song rate, song type, and song perch height vary in relation to breeding stage in a year-round resident songbird.

According to the territory defence hypothesis, birds sing to announce occupancy of utilized space (Szymkowiak and Kuczyński 2017, Mejías et al. 2021, Wheeldon et al. 2021). 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), providing strong support for the territory defence hypothesis. If song is indeed important in territory defence, then a non-migratory passerine that never leaves its territory vacant should sing year-round to defend it.

Avian song is also hypothesized to be important in mate attraction (Kroodsma 1984, Catchpole and Slater 2003, Sockman et al. 2005). In line with the mate attraction hypothesis, vocal output can be higher among unpaired males than paired males (Staicer et al. 2006, Liu and Kroodsma 2007). Bachelor males often sing at higher rates at dawn (e.g. savannah sparrows, *Passerculus sandwichensis*; Moran et al. 2019), but then reduce daytime song once paired (e.g. chipping sparrows, *Spizella passerine*; Liu and Kroodsma 2007). Indeed, singing should significantly decline or cease following mate acquisition if the goal of singing is to advertise the signaler's availability to breed. Despite the soundness of the mate attraction hypothesis, studies in which the singing rates of males are correlated with their pairing status are rare in most avian families and thus should be conducted in additional taxa.

In addition to becoming vocally conspicuous, birds might advertise their willingness to breed by increasing their visibility. For example, 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. Previous research has 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); this avenue of research has yet to be explored in most passerine species.

The white-eyed vireo *Vireo griseus* is an ideal model with which to test these hypotheses. It is a small songbird inhabiting shrublands and thickets in the southeastern USA. Only males sing, and they produce two distinctive song types: 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 (Mejías et al. 2021); 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. 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 an endemic breeder on the Bermuda archipelago (Bangs and Bradlee 1901, Mejías et al. 2021). It rears one brood per season, although pairs can make up to five breeding attempts per year following nest failure (Mejías 2021). Like its continental counterpart, only males sing discrete and rambling songs (M. Mejías pers. obs.). Although Bermuda vireo songs have been studied from the perspective of receivers (Mejías et al. 2021), the current study is the first to quantify the singing behaviour of signalers.

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 hypothesis, 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. 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 breeding males without nesting duties than for breeding 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).

Material and methods

Study site and study species

Bermuda is a remote island (32°18′N, 64°47′W) with low-lying yet hilly terrain (0–76 m, mean: 38 m) and 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). Present-day wooded habitat in Bermuda is dominated by invasive secondary forest (Mejías and Nol 2020, Mejías and Mejías 2020). Amongst our two study sites, Spittal Pond Nature Reserve (24 ha) and Ferry Reach Park (26 ha) (Fig. 1), flora include 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*. Current songbird avifauna comprises nine species, including the Bermuda vireo, and most breed from March–September (pers. obs.).

In May 2018, January 2019, and April 2019, we captured 10 male vireos and four 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 or rambling song (known only in males; Bradley 1980) as they approached the mist net or during follow-up observations (below). Female response to playback 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 four previously colour-banded vireos (two males and two females) living at Ferry Point Park. In total, we had 12 colour-banded males that served as our focal subjects (Spittal Pond: seven males; Ferry Point Park: five males). All six 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 h per day and taking GPS coordinates of used perches. We marked the GPS coordinates of several perches with a handheld GPS unit. In general, the territories where birds were captured 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

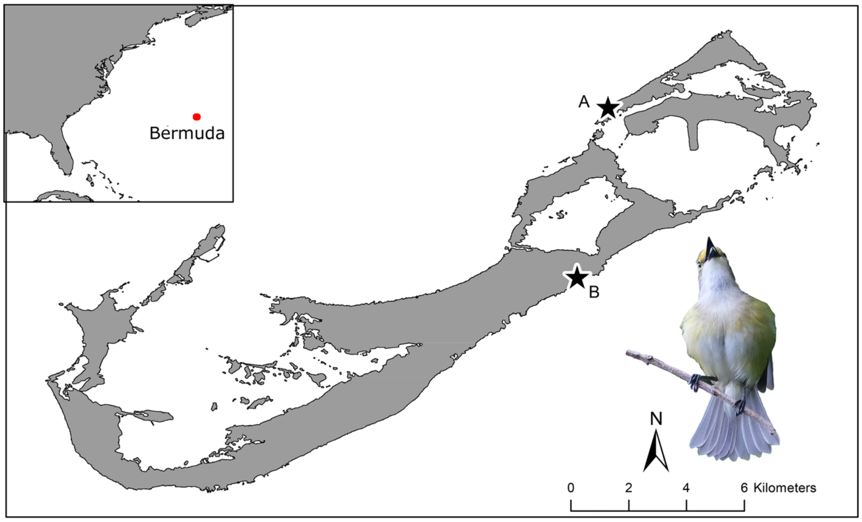

Figure 1. Two sites in Bermuda where 12 colour-banded male Bermuda vireos were recorded throughout the breeding and non-breeding seasons: (A) Ferry Reach (n = 5 males) and (B) Spittal Pond (n = 7). Photograph by Andrea Webb.

our study, approx. 100 m away, and 2) a male we banded in December 2018 and that was present for the entire 2019 breeding season 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 (07:00–12:00 h) singing behaviour of the 12 male birds throughout most of the subspecies' breeding season (April 2019–August 2019). Of these 12 males, we found and re-recorded 11 during 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 15:00 h (M. Mejías pers. obs.). 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 five times during the nonbreeding season. We visited the Spittal Pond site 44 times during the breeding season and seven times during the non-breeding season. We had greater sampling effort during the breeding season because our winter residency on the island was limited compared to the summer months, and because the breeding season was subdivided into five breeding stages ('Breeding stage' below). While at a site, we recorded each male inside his territory during a separate 15 min recording session throughout the morning. The 15 min recordings were long enough that they often contained multiple singing bouts from the focal male, thus allowing us to estimate his song rate with reasonable accuracy, yet short enough that we could record all males at the site in the same 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 repertories 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.

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 ± 1 m) any remaining height of the tree above the fully extended pole. Unfortunately, severe foliage damage from Hurricane 'Humberto' in September 2019 (i.e. between our breeding season and non-breeding season song recordings) reduced the maximum heights of measured trees inside surveyed territories. All 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 (13:00–17:00 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; Mejías 2021). We defined nest building as the stage when vireos are adding material 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, and because separation of bonded pairs occurs in this subspecies, 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). Therefore, 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. Whenever possible, we identified and reported the causes of nest failure, for descriptive purposes. 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). 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.

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 (ver. 1.5; 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 (Mejías et al. 2020, Mejías et al. 2021). Our song definition did not hinder our ability to identify discrete songs and rambling songs (Fig. 2), as defined by Bradley (1980; Fig. 1B, 2A–C). In total, we annotated 17 682 vireo songs from 430 15 min recordings. Details of how recordings and annotated songs are distributed among males and between the breeding and non-breeding seasons are provided in Table 1.

Statistical analyses

Statistical analyses were conducted using R (ver. 3.5.2; www.r-project.org, R Foundation of Statistical Computing, Vienna, Austria). In our first set of analyses, we used generalized linear mixed-effect hurdle models (glmmTMB package; Brooks et al. 2017) to compare the number of songs per 15 min recording session between breeding stages. Separate models were used to compare the number of discrete songs per session and the number of rambling songs per session between the breeding season (includes no nesting duties, nest building, incubation, nestling care, and fledgling care) and non-breeding season. Two additional models compared the number of discrete songs per session and the number of rambling songs per session between the no nest duty and nest duty stages of the breeding season. In each model, we included the number of discrete songs or the number of rambling songs per 15 min recording session as the dependent variable, the breeding stage (i.e. breeding season versus non-breeding season or no nesting duties versus nesting duties) 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. Hurdle models split the variation in the response variable into two components: the first uses a binary model to model whether the response is zero or positive (i.e. whether it clears the hurdle), and the second uses a truncated distribution to model the positive responses (Feng 2021). Hurdle models assume that zero and positive responses represent separate underlying processes (Feng 2021). In our case, the zeros represent birds that chose to not sing, whereas the positive values represent variation in the number of songs produced among those individuals that chose to sing. The positive responses were modeled with a negative binomial distribution and log link.

In our second set of analyses, we used three generalized linear mixed-effect models to investigate the factors associated with song perch height. In all three models, the song perch height (m) of each song was included as the dependent variable and was modeled using a negative binomial distribution with log link. Recording session (1–32) nested within subject identity (1–12) was included as a random effect to account for possible dependencies among multiple perch heights estimated from the same recording session of the same male. Season (breeding versus non-breeding) was included as a fixed effect in the first model and song type (discrete versus rambling) as a fixed effect in the second model. We did not include season and song type in the same model because the sample sizes were extremely unbalanced (77 rambling songs

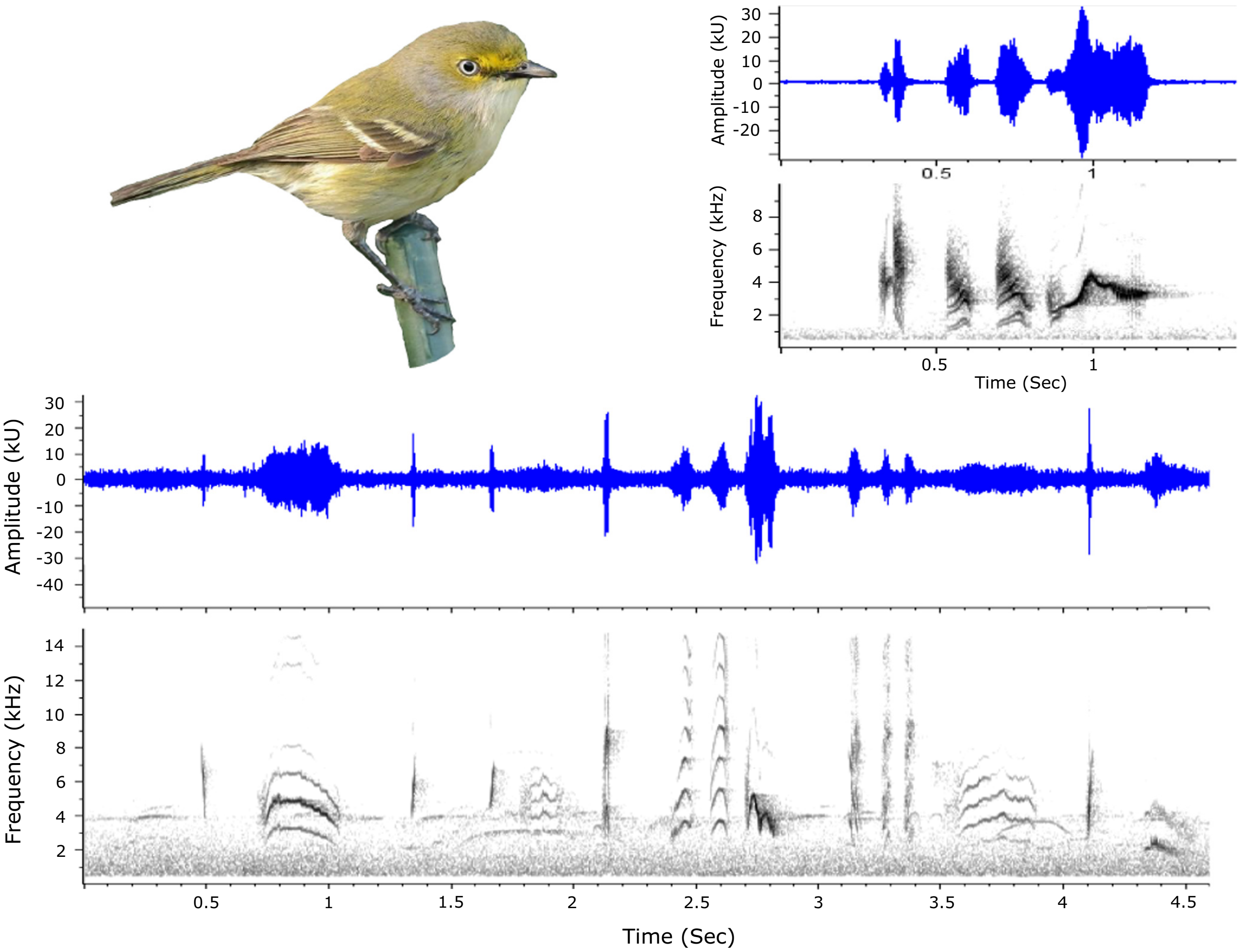

Figure 2. Waveforms and spectrograms depicting the two song types of male Bermuda vireos: discrete song (top right panels) and rambling song (bottom panels). The discrete song is short (ca 1 s) and comprises highly modulated elements, including chips, buzzes, and whistles delivered in a fixed sequence; males generally 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 (s). Photograph by Richard Brewer.

versus 1871 discrete songs in the non-breeding season and 787 rambling songs versus 14947 discrete songs in the breeding season) and could yield effects that were not representative of rambling songs. The third model focused on the subset of data derived from the breeding season and included nest duties (with versus without) as the fixed effect.

Results were considered statistically significant where $p < 0.05$. We used the DHARMa package (Hartig 2020) to validate all statistical models. Its diagnostic tests, combined with visual inspection of scaled residual plots, indicated adequate model fit in all cases. 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; Table 1), equating to 6450 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

Table 1. Number of recording sessions, discrete songs, and ramblings songs recorded from colour-banded, male Bermuda vireos during the breeding season (n = 12 males) and non-breeding season (n = 11 males). The superscripts under 'Total Recordings' denote the total number of recordings during the breeding (B) and non-breeding (NB) seasons. The values in parenthesis under the remaining columns denote the minimum and maximum number of songs per male in each season. NA denotes a male that had disappeared before the non-breeding season.

Male ID	Total Recordings	Discrete songs Breeding	Discrete songs Non-breeding	Rambling songs Breeding	Rambling songs Non-breeding
All birds (n = 12)	430 (374^{B}; 56^{NB})	14947 (0–209)	1871 (0–175)	787 (0–56)	77 (0–56)
BlackWhiteBlue	42 (37^{B}; 5^{NB})	467 (0–58)	131 (7–49)	2 (0–2)	0 (0–0)
BlueBluePink	39 (34^{B}; 5^{NB})	1155 (0–128)	254 (12–94)	25 (0–21)	0 (0–0)
BlueGreen	30 (30^{B}; 0^{NB})	574 (0–63)	NA (NA)	140 (0–45)	NA (NA)
BlueRed	38 (33^{B}; 5^{NB})	1315 (0–136)	8 (0–6)	151 (0–40)	0 (0–0)
GreenOrange	32 (26^{B}; 6^{NB})	1204 (0–131)	240 (3–105)	49 (0–30)	56 (0–56)
GreenRed	34 (29^{B}; 5^{NB})	1466 (0–178)	159 (17–46)	31 (0–27)	17 (0–17)
OrangePurple	39 (34^{B}; 5^{NB})	879 (0–87)	76 (0–41)	77 (0–47)	0 (0–0)
Pink	35 (30^{B}; 5^{NB})	1226 (0–156)	138 (4–62)	52 (0–31)	0 (0–0)
Purple	36 (31^{B}; 5^{NB})	1102 (0–154)	102 (0–77)	79 (0–51)	0 (0–0)
RedPink	33 (28^{B}; 5^{NB})	2541 (0–209)	258 (29–85)	20 (0–11)	4 (0–4)
WhiteGreen	37 (32^{B}; 5^{NB})	2083 (0–172)	0 (0–0)	102 (0–53)	0 (0–0)
YellowBlue	35 (30^{B}; 5^{NB})	935 (0–116)	505 (16–175)	59 (0–56)	0 (0–0)

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 (Table 1). Discrete song rate was fairly constant throughout the breeding and non-breeding season, with the lowest rates recorded in August (Fig. 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. 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 nest predation

All 12 males made at least one breeding attempt (3 ± 1 nests; 1–5), but only three 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 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.

Song production in relation to breeding stage

Hurdle models show that the probability of producing at least one discrete song during a given 15 min recording session did not differ significantly between the breeding (303 of 374 recording sessions, or 81%) and non-breeding season (46 of 56 sessions, or 82%; $z = -0.17$, $p = 0.862$). Similarly, among recording sessions in which the focal male produced at least one discrete song, the number of discrete songs produced did not differ significantly between the breeding and non-breeding season ($z = -1.21$, $p = 0.225$; Fig. 4). The probability of producing at least one rambling song also did not differ significantly between the breeding (46 of 374, or 12%) and non-breeding season (3 of 56 sessions, or 5%; $z = 1.48$, $p = 0.139$). For those sessions in which the subject did produce rambling songs, the number of rambling songs did not differ significantly between the breeding and non-breeding season ($z = 0.61$, $p = 0.543$).

Within the breeding season, subjects were significantly more likely to produce at least one discrete song when they did not have nest duties (129 of 146 recording sessions, or 88%) than when they had nest duties (164 of 218 sessions, or 75%; $z = 2.77$, $p = 0.006$). Furthermore, among the recording sessions in which subjects produced discrete song, the number of discrete songs was higher if the male did not have nest duties ($z = -2.55$, $p = 0.011$; Fig. 4, 5). In contrast, the probability of producing at least one rambling song did not differ significantly between males with nest duties (24 of 218 sessions, or 11%) and males without nest duties (22 of 146 sessions, or 15%; $z = 1.15$, $p = 0.252$). Among the recording sessions in which subjects produced rambling song, the number of rambling songs did not differ significantly between males with nest duties and males without nest duties ($z = -0.53$, $p = 0.593$).

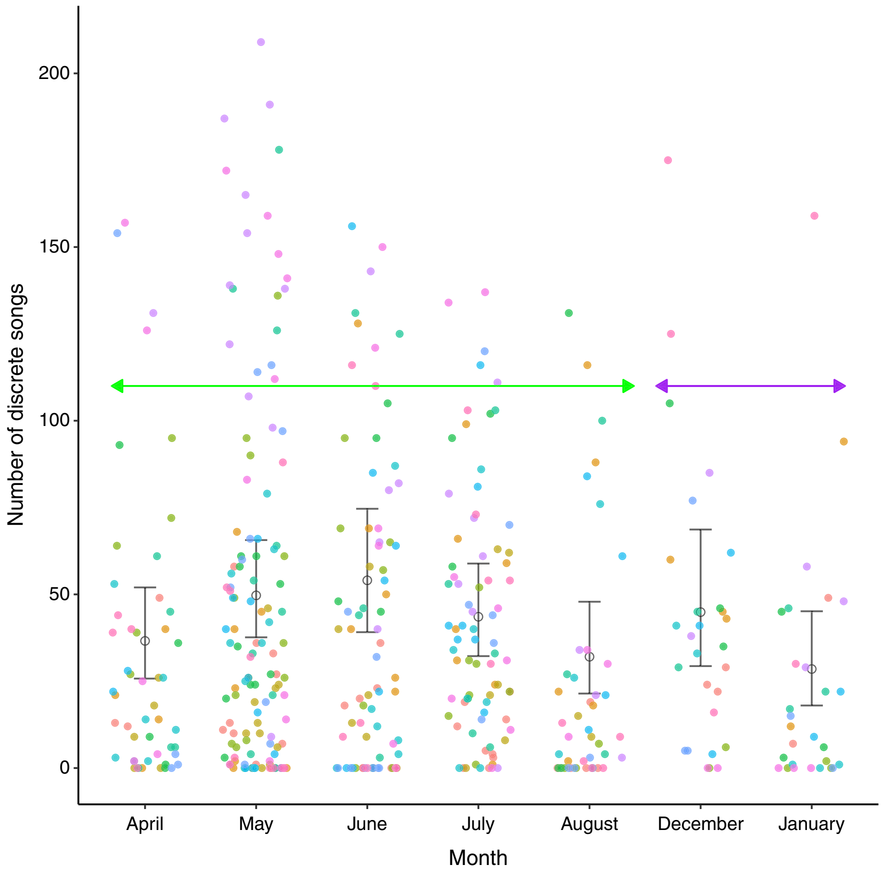

Figure 3. Number of discrete songs produced during 15-min recording sessions of male Bermuda vireos during the breeding season (April – August; green arrow) and non-breeding season (December–January; purple arrow). Estimated marginal means and 95% confidence intervals derived from a generalized linear mixed-effect hurdle 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. Estimated marginal means and 95% confidence intervals were derived using the '*ggeffect*' function of the ggeffects package (Lüdecke 2018) in R (www.r-project.org). Different coloured dots correspond to different colour-banded male Bermuda vireos recorded during the study.

Factors associated with song perch height

We estimated song perch heights for 6793 of the 17 682 (34%) songs recorded. Males sang from a wide range of perch heights (Fig. 6, Supporting information), but rarely sang from the tallest available perches (Supporting information). Song perches were significantly higher during the breeding season than during the non-breeding season ($z = -10.96$, $p < 0.001$; Fig. 6A), for breeding males with no nesting duties than for breeding males with nesting duties ($z = -9.67$, $p < 0.001$; Fig. 6B), and for males singing discrete songs versus rambling songs ($z = -4.57$, $p < 0.001$; Fig. 6C.).

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, but the number of songs produced did not differ between the breeding and non-breeding seasons for either song type. During the breeding season, however, males with nesting duties sang fewer discrete songs than males without nesting duties. 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, Nolan 1960, Graber 1961, Nolan 1962, James 1978, Bradley 1980, Robinson 1981, Gomez-Montes and Moreno 2008, Hedley 2016); for *V. griseus*, 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

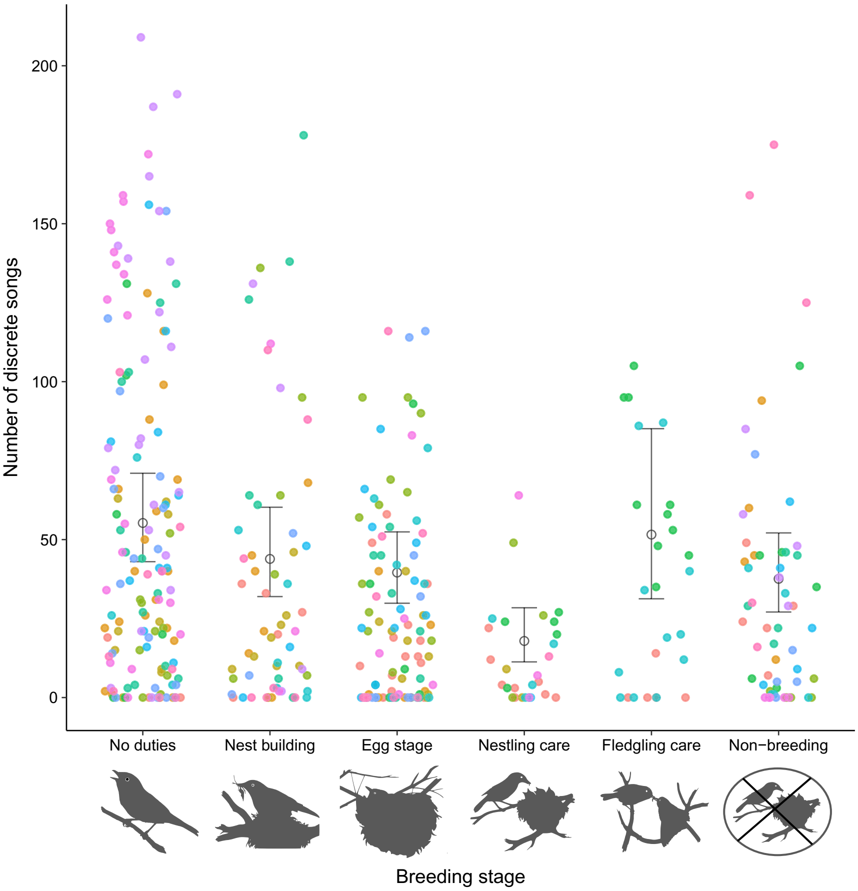

Figure 4. Number of discrete songs produced during 15-min recording sessions of male Bermuda vireos during six breeding stages: 1) no nesting duties, 2) nest building, 3) egg stage, 4) nestling care, 5) fledgling care, and 6) non-breeding. Estimated marginal means and 95% confidence intervals derived from a generalized linear mixed-effect hurdle model (discrete song rate was included as the dependent variable, with breeding stage 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 breeding stage. Estimated marginal means and 95% confidence intervals were derived using the '*ggeffect*' function of the ggeffects package (Lüdecke 2018) in R (www.r-project.org). Different coloured dots correspond to different colour-banded male Bermuda vireos recorded during the study. Vireo silhouettes were drawn by Michelle Pasquin.

seasons suggests that it 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), but our analyses also suggest that its production does not differ between seasons. Furthermore, 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 countersinging 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 and singing locality 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 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

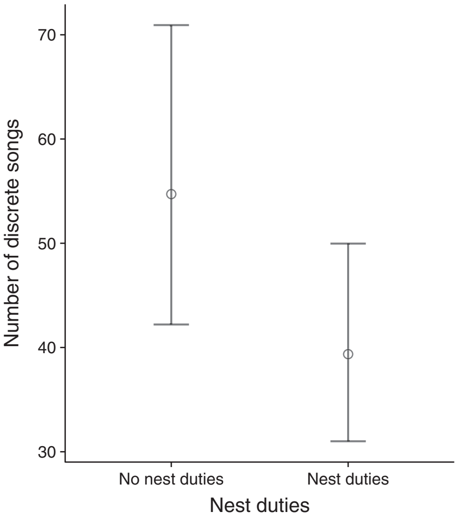

Figure 5. Number of discrete songs produced during a 15-min recording session by breeding males with and without nest duties. Males were considered to have nest duties if they were categorized as being in the nest building, egg, nestling care, or fledgling care stage. Estimated marginal means and their 95% confidence intervals were derived using the '*ggeffect*' function of the ggeffects package (Lüdecke 2018) in R (www.r-project.org).

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. Field observations of Bermuda vireos (Mejías 2021) provide further support that singing from elevated perches is a mechanism for attracting prospective females: 1) breeding pairs travel primarily in the understory, 2) nests are never built in the canopy, but, rather, from forked branches, usually 2–3 m above the ground, and 3) males often return to canopy perches after their mate disappears, 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 described subjectively as being 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).

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.), 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). Lastly, future work should test whether nest predation risk could explain differences in song rate across nesting stages.

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.

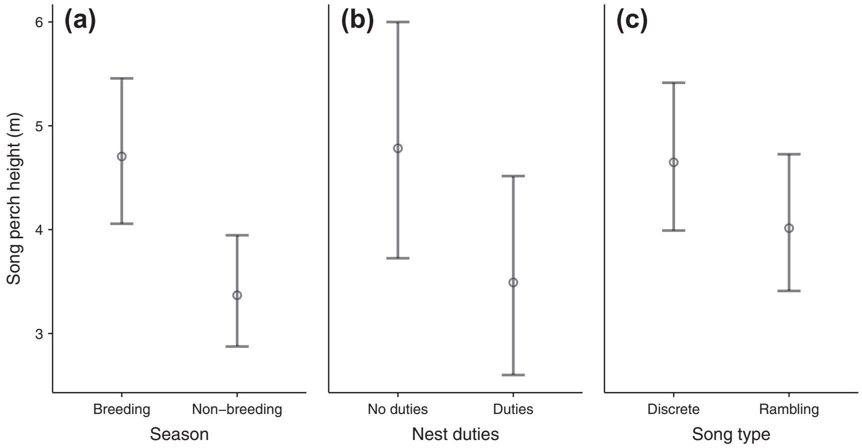

Figure 6. Song perches of male Bermuda vireos were higher (a) in the breeding season than in the non-breeding season, (b) among males with no nesting duties than among males with nesting duties during the breeding season, and (c) when males sang discrete songs versus rambling songs. Estimated marginal means and 95% confidence intervals derived from generalized linear mixed models (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 is not shown in this figure.

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Author contributions

Miguel Mejías: Conceptualization (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **David Wilson**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Resources (lead); Software (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.47d7wm3k0 (Mejías and Wilson 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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Table S1. Heights (m) of song perches used by male Bermuda Vireos during the non-breeding season ($N = 11$ males), as well as 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 median, minimum–maximum perch heights observed, the sample size, and the heights and species of the two tallest trees in his territory. 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 the maximum song perch height for this individual was measured during the 2019 breeding season, before a severe hurricane destroyed the tallest trees in his territory. Our measures of the tallest trees were made after the hurricane.

Male Colour Band ID	**Singing Heights (m)**			**Tallest 2 Trees in Territory (m)**
	Non-breeding Season (m)	**Breeding Season – No Nesting Duties**	**Breeding Season – Nesting Duties**	
BlackWhiteBlue	5; 4–5; 8	3; 3–5; 8	4; 1–12; 133	15^{CA}; 20^{CA}
BlueBluePink	4; 2–6; 68	5; 1–14; 368	4; 2–6; 96	13^{CA}; 15^{CA}
BlueGreen	NA	5; 1–7; 168	4; 1–8; 126	16^{CA}; 18^{CA}
BlueRed	2; 1–3; 5	7; 2–9; 63	5; 1–8; 597	**10^{SH};14^{BC}**

GreenOrange	5; 2–7; 121	5; 2–7; 130	5; 1–8; 396	9^{FW};11^{CA}
GreenRed	3; 1–5; 43	2; 1–14; 331	5; 1–10; 405	18^{CA}; 21^{CA}
OrangePurple	3; 1–6; 42	2; 1–5; 56	3; 1–10; 380	14^{CA}; 15^{CA}
Pink	2; 1–3; 8	4; 1–5; 246	3; 1–6; 118	$11^{\mathrm{IL}}13^{\mathrm{CA}}$
Purple*	NA	3; 1–8; 199	4; 1–14; 65	10^{FW};10^{FW}
RedPink	3; 1–6; 88	8; 1–17; 1285	4; 1–12; 128	17^{CA}; 18^{CA}
WhiteGreen	NA	9; 1–14; 701	6; 1–8; 162	13^{CA}; 15^{CA}
YellowBlue	2; 1–8; 66	3; 1–12; 46	3; 1–9; 85	15^{CA}; 22^{CA}

Values in bold indicate the heights of native trees. Superscript initials correspond to the following tree species: Bermuda Cedar (BC), Casurina (CA), Fiddlewood (FW), Indian Laurel (IL), and Southern Hackberry (SH).