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ORIGINAL ARTICLE

Song variation across space and time in Anna's Hummingbird (*Calypte anna*)

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Abstract

Birds use song to communicate in multiple contexts, including territoriality and courtship. Of particular interest is the phenomenon of song sharing, in which direct neighbors' songs are more similar to one another than those of non-direct neighbors. Song sharing has been studied extensively in oscine songbirds. However, despite the high diversity of hummingbird vocalizations, less attention has been given to this lineage. Anna's Hummingbird (*Calypte anna*) has a spectrally complex, three-phrase multisyllabic song that varies on both macrogeographic and microgeographic scales. In this study we tested for song sharing between neighbors and for an effect of physical distance on song distance within a single population. In January and February of 2021, we audio recorded 29 Anna's Hummingbirds in Golden Gate Park, San Francisco, CA. We characterized syllable types, and measured spectral and temporal features of songs in Raven Pro 1.6. We evaluated how Anna's Hummingbird song form may change over time by comparing our results to those of a study conducted at the same site in 1999 and recordings from the 1980s. In our recordings from 2021, we identified 25 syllable types and eleven song types, and found evidence for both syllable and song type sharing between males with adjacent territories. We found high turnover of syllable types between the 1980's and 2021, demonstrating the potential for rapid cultural evolution in hummingbird song.

Keywords *Calypte anna* · Songlearning · Micro geographic variation · Song neighborhoods

Zusammenfassung

Gesangsvariation in Raum und Zeit beim Annakolibri *(Calypte anna)*

Vögel nutzen ihren Gesang zur Kommunikation in verschiedenen Kontexten, darunter zur Markierung ihres Reviers und zur Balz. Von besonderem Interesse ist das Phänomen des „Song Sharing", bei dem die Gesänge direkter Nachbarn einander ähnlicher sind als die von nicht-direkten Nachbarn. Das „Song Sharing" wurde bei Singvögeln der Familie der Oscines (Passeriformes) bereits umfassend untersucht. Trotz der hohen Vielfalt an Lautäußerungen bei Kolibris wurde dieser Abstammungslinie jedoch bisher weniger Aufmerksamkeit geschenkt. Der Annakolibri (*Calypte anna*) verfügt über einen spektral komplexen, aus drei Phrasen bestehenden, mehrsilbigen Gesang, der sowohl auf makrogeografischer als auch auf mikrogeografischer Ebene variiert. In dieser Studie untersuchten wir das „Song Sharing" zwischen Nachbarn sowie den Einfluss der physischen Entfernung auf die Gesangsähnlichkeit innerhalb einer einzelnen Population. Im Januar und Februar 2021 nahmen wir 29 Annakolibris im Golden Gate Park in San Francisco, Kalifornien, akustisch auf. Wir charakterisierten Silbentypen und maßen spektrale und zeitliche Merkmale der Gesänge in Raven Pro 1.6. Wir untersuchten, wie sich die Gesangsform des Annakolibris im Laufe der Zeit verändern könnte, indem wir unsere Ergebnisse mit denen einer 1999

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am selben Ort durchgeführten Studie sowie mit Aufnahmen aus den 1980er Jahren verglichen. In unseren Aufnahmen aus dem Jahr 2021 identifizierten wir 25 Silbentypen und elf Gesangstypen und fanden Hinweise darauf, dass Männchen mit benachbarten Revieren sowohl Silbentypen als auch Gesangstypen miteinander teilen. Wir stellten zwischen den 1980er Jahren und 2021 einen hohen Wechsel der Silbentypen fest, was das Potenzial für eine schnelle kulturelle Evolution im Gesang von Kolibris zeigt.

Introduction

How, why, and when birds learn their songs are enduring questions in animal behavior. Song learning has evolved in at least three avian clades: the oscine songbirds, parrots, and hummingbirds (Nottenbohm 1972; Janik and Slater 1997; Tyack 2019; Janik and Knörnschild 2021). Subject to errors and improvisation, learned song can facilitate song variation, and the formation of song types that can be stable or labile over time. Most research on avian song has focused on oscine songbirds (Slater 1981; Baker and Cunningham 1985; Tsipoura and Morton 1988; Ellers and Slabekoorn 2003; DeVoogd et al. 1993; Podos and Warren 2007). Despite having complex and diverse songs, hummingbirds have received less attention and few studies have evaluated whether and how hummingbird songs may change over time.

Like the songs of oscines, hummingbird songs can vary on both micro- and macrogeographic scales (Snow 1968; Wiley 1971; Baptista and Schuchmann 1990; Gaunt et al. 1994; González and Ornelas 2009, 2014; Araya-Salas and Wright 2013; Lara et al. 2015; Araya-Salas et al. 2019; Berger et al. 2025). One mechanism that can generate microgeographic variation in song is song sharing between birds with neighboring territories (Payne et al. 1988; Hill et al. 1999). Song sharing, and the associated formation of song neighborhoods in which sub-sets of locally aggregated individuals share song-types, is widespread in oscines (Payne 1985; McGregor and Thompson 1988; Hughes et al. 1998) and is documented in several neotropical hummingbird species (e.g., Wedge-tailed Sabrewings [*Pampa curvipennis*]: González and Ornelas 2009, Hermit Hummingbirds [*Phaethornis*]: Snow 1968; Wiley 1971; Snow 1974; Stiles and Wolf 1979; Araya-Salas and Wright 2013). To our knowledge, only two studies in hummingbirds have evaluated whether shared song types change over time in the wild. In Wedge-tailed Sabrewings, song neighborhoods were stable over the course of a four-year study with a low rate of syllable type turnover within each neighborhood (González and Ornelas 2009). In contrast, the monosyllabic song types of Long-billed Hermits (*Phaethornis longirostris*) had turnover rates of a few months in some males (Araya-Salas and Wright 2013). These contrasting patterns of song stability and plasticity within single generations highlight the need for temporal studies in a wider range of hummingbird species, and raise the question of how hummingbird songs may change across time periods longer than individual lifetimes.

We set out to fill this gap in a song-learning hummingbird species, Anna's Hummingbird (*Calypte anna*; hereafter Anna's). Male Anna's learn their songs (Baptista and Schuchmann 1990) and sing during territorial and courtship displays (Wells et al. 1978; Stiles 1982; Clark and Feo 2008, 2010). Anna's song is spectrally complex with three multi-syllabic phrases (A–C) that are integrated into both static and dynamic multimodal courtship displays. The first phrase of the song (phrase A), is sung repeatedly as part of two dynamic courtship displays, the dive-display, in which a male hovers while singing phrase A and subsequently dives towards females while sonating (Clark and Feo 2008), and in a circling display, in which a male repeatedly flies around the female, flying low to the ground and then up to a perch where he sings phrase A while flaring his gorget (Stiles 1982). The full song (phrases A–C) is sung from perches and in flight during territorial chases. In this study we focused on static perched song. Previous studies have found the highest inter-individual variation in phrase A and syllable type sharing patterns suggestive of song learning on the syllable level (Yang et al. 2007; Berger et al. 2025).

Anna's Hummingbird song varies between populations in both syllable usage and spectral and temporal components (Berger et al. 2025), and syllable usage can vary within population (Yang et al. 2007). Yang et al. (2007) found that, in 1999, there was a weak negative association between syllable types used and between-bird distance, indicating that birds with adjacent territories tend to share syllables (Yang et al. 2007). Here, we characterize the spatial distribution of song and syllable types in the same single population studied by Yang et al. (2007) and evaluate temporal change in syllable types across multiple generations. To do so, we sampled an Anna's population in Golden Gate Park (San Francisco, CA, USA) that was recorded at three earlier time points: March 1985 and August 1987 (LF Baptista and K-L Schuchmann, archived in the Borror Laboratory of Bioacoustics), and April to May 1999 (Yang et al. 2007). We 1) identify syllable types and song types, 2) determine the spatial distribution of song sharing and test the effect of inter-individual distance on song distance, based on both syllable type usage and temporal and spectral measures, as well as 3) evaluate the extent of syllable type turnover across decades. Documenting spatial patterns of song sharing provides insight into the social

mechanism and function of song-learning. Furthermore, documenting how songs in a single population may change over time helps to connect population level variation to the evolution of among-population differences in song.

Methods

Recording

We sampled Anna's song from Golden Gate Park, (San Francisco, CA, USA), a 1,000 acre urban public park. Recordings were collected in January and February 2021 during the January to June breeding season ($n = 29$ birds, Fig. 1b, electronic supplementary material Table S1). We recorded songs from males singing on their breeding territories (5–30 songs/male). Breeding males have stable territories and can be identified by perch fidelity (Stiles 1973; Stiles 1982; Clark and Russell 2012). Recordings from a given male were collected consecutively over the course of one day. Recordings were captured with a Zoom F8 multitrack field recorder (Zoom Corporation, Tokyo, Japan), at a sample rate of 48 kHz with a 24-bit depth using a Sennheiser ME 62 omnidirectional microphone head with a K6 powering module (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany; frequency range 30 Hz–20 kHz, ± 1 dB) and a parabola shell (Wildtronics, LLC Mono Parabolic microphone, Newton Falls, OH, USA) at a distance of up to 15 m from the focal bird. GPS coordinates were taken using an iPhone 11 ios 15 and the application Gaia GPS v2020.6 (Trailbehind Inc., Berkeley, CA, USA) with positional accuracy of three to five meters. Straight line distance between individuals was calculated using the Haversine formula in the *R* package *geosphere* (Hijmans et al. 2022; https://CRAN.Rproject.org/package=geosphere).

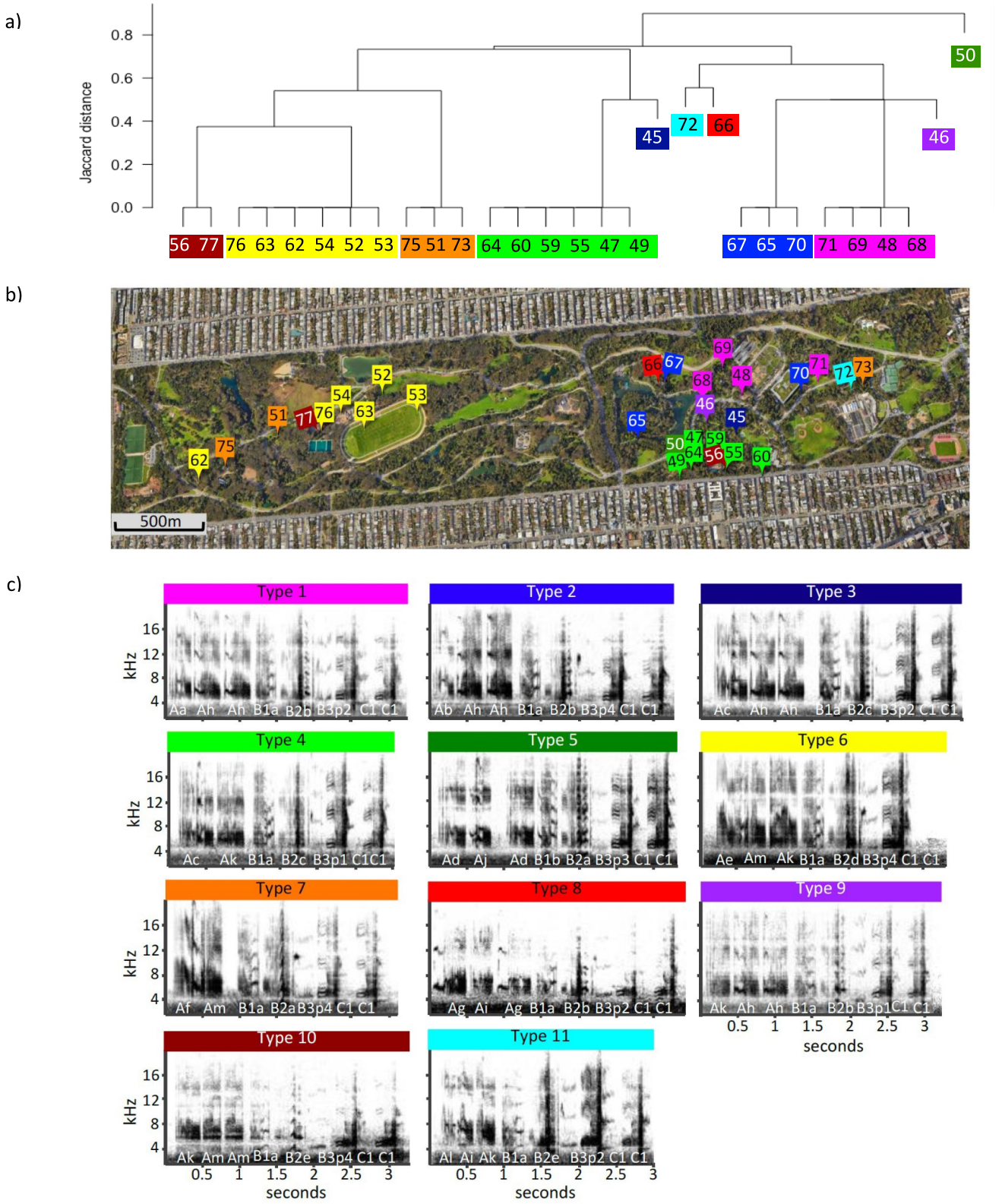
We obtained recordings of male Anna's made in March 1985 ($n = 2$ males) and August 1987 ($n = 7$ males) by LF Baptista and K-L Schuchmann, archived in the Borror Laboratory of Bioacoustics (blb.osu.edu/database/; The Ohio State University; electronic supplementary material Table S1). Analysis of spectrograms from 1999 ($n = 35$ males) was from the published paper as recordings were not available (Yang et al. 2007). Spectrograms presented in the paper used a window size of 512 (Yang et al. 2007), which we replicated. Recordings from both the 1980's and 1999 were captured using a Nagra tape recorder and ME 20 Sennheiser microphone (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany; frequency range 50 Hz–15 kHz, ± 3 dB). Digitization of analog recordings from the 1980's was done by the Borror lab of Bioacoustics using an instrumentation-grade converter with 16 bit amplitude resolution and 48,000 samples per second. To avoid any potential effects of analog to digital conversion on spectral and temporal measures, we limited our comparisons to classifications of syllable form.

Song analysis

Anna's song is complex with high entropy and a frequency range of 1.5 kHz to 20 kHz, with most of the energy between 1.5 kHz and 4 kHz. As in Berger et al. (2025), we divided the songs into phrases, syllables, and elements by visual inspection of the spectrograms generated in *Raven Pro* v1.6 (Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA) using a 512 FFT smooth Hamming window. Anna's song consists of three multi-syllabic phrases (A–C; Fig. 2). Phrase A consists of two to four syllables, phrase B consists of two to three syllables, and phrase C consists of one to two syllables. We defined syllables as repeatable components that have an inter-syllable interval less than 0.08 s and defined phrases as repeated groupings of syllables with between-phrase intervals greater than 0.08 s (Berger et al. 2025). We used the same designation and nomenclature for phrases as Yang et al. (2007) with the exception of phrase B, which comprised three syllables in 2021 as opposed to two (see results). We used our own nomenclature for syllables.

We defined song types as songs that share all syllable types (Tsipoura and Morton 1988; electronic supplementary material Fig. 1). We visually evaluated ten songs per male, both within a song bout in consecutively produced songs and across multiple song bouts, to check whether the presence/absence of each syllable type was consistent within individual. Whereas repetition of phrases within a song varied within individual depending on context, with phrase A sometimes repeated multiple times before continuing to phrases B and C, there was no variation in the syllable types used or in the order of phrases a given male sang (i.e., phrase B followed phrase A and phrase C followed phrase B). Thus, we found no evidence that individuals have repertoires of more than one song type. Therefore, we selected the song with the highest signal to noise ratio and the lowest background noise to represent each male.

We collected a total of 23 quantitative measurements for each song (Table 1; Fig. 2), with particular focus on properties of the song that were tonal and had similar components across all songs (e.g., upper whistle peak frequency in syllable B1, B3 pulse measurements, and peak frequency of pulses and lower and upper tones in C1). A single observer (WWY) measured the duration and peak frequency of each syllable in *Raven Pro* v1.6 (Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA) using a 512 FFT smooth Hamming window and manual selection (the 'by-eye' method). All measurements were taken on the 1st harmonic. Syllables B3 and C1 had biphonic tones, for which we measured each dominant frequency separately



(Table 1; Fig. 2). Peak frequency, the frequency (in kHz) with the highest amplitude, was calculated automatically in *Raven Pro*. Given the high frequency of Anna's songs, the high signal to noise ratio of most recordings, and the clear onset and offset of the signals, we are confident that

◂**Fig. 1** Anna's Hummingbird (*Calypte anna*) males ($n = 29$) recorded in Golden Gate Park in 2021. **a** Dendrogram illustrating hierarchical clustering of syllable usage, individuals colored by their visually assigned song type; numbers are individual IDs. **b** Locations of the 29 individuals colored by song type. Individual IDs are indicated; map from Google Earth. **c** Representative spectrograms for eleven song types. Colors correspond to the dendrogram and map locations of males that sang a given song type. Representative songs can be found on Xeno-Canto: Type 1 (XC958868); Type 2 (XC1041009); Type 3 (XC958864); Type 4 (XC958875); Type 5 (XC958870); Type 6 (XC958872); Type 7 (XC958872); Type 8 (XC1041010); Type 9 (XC958865); Type 10 (XC958876); Type 11 (XC1041016)

our measurements were robust to the potentially subjective nature of the by-eye method.

To define distinct syllables, a single observer (ANB) visually cataloged syllables through inspection of the spectrograms with the bird IDs hidden (Searcy et al. 1985; Podos et al. 1992; González and Ornelas 2009). We did the same with recordings from 1985 and 1987. To check the repeatability of the syllable designations, this process was repeated four times for each song by the same observer. We calculated the intraclass correlation coefficient (ICC) with 95% confidence intervals using the *icc* function in the *R* package *irr* (Gamer et al. 2025; https://CRAN.R-project.org/package=irr) based on a one-way mixed-effects model. Although intraobserver classification is generally more consistent than interobserver classification (Boyce et al. 2000), it remains susceptible to observer-specific biases that may influence estimates of syllable repertoire size. We sought to minimize such biases by scoring spectrograms blind of individual information, repeating classifications at intervals of months to years part, and conservatively defining syllable types as distinct only when differences were clear and discrete. We also made visual comparisons between our catalog of syllable types and those defined by Yang et al. (2007) in their Fig. 4. However, the high entropy, broadband, and atonal nature of phrase A syllables made visual comparisons to the published spectrograms in Yang et al. (2007) difficult. We therefore took a conservative approach and compared only the B and C phrases across all three time periods. Because we had access to the recordings from the 1980's, we were able to include Phrase A in the spectral comparisons with 2021.

To evaluate how well our sampling represented all syllable types in the 2021 population, we plotted a rarefaction curve of the number of syllables identified in the songs of the 29 males we recorded and randomly permutated the order of individual samples using the *specaccum* function in the *R* package *vegan* (Oksanen et al. 2018; https://CRAN.R-project.org/package=vegan). We then calculated the number of samples needed to achieve the asymptotic maximum number syllable types using the Lomolino model (Lomolino 2000) in the *R* package *vegan*. We did the same for the nine birds sampled in the 1980's.

To test for an effect of physical distance between males on syllable use, we used the presence/absence of each syllable type in the representative full song of each male to produce a Jaccard dissimilarity matrix with the *R* package *vegan* (Oksanen et al. 2018). To test for an effect of between male distances on spectral and temporal measurements we entered all measurements into a principle component analysis (PCA) and used PC1—3 scores for each individual to calculate Euclidian distance (song distance). Correlations between syllable use distance and physical distance, and between song distance and physical distance, were tested with Mantel tests (10,000 iterations) in *XLSTAT* (Lumivero, Burlington, MA, USA). PCA was run in *JMP* (SAS Institute Inc., Cary, NC, USA).

To test for songtype neighborhoods, we visually catalogued song types. To evaluate spatial relationships among songtypes, we ran a hierarchical cluster analysis on the Jaccard dissimilarity matrix for syllable types with the average linkage method. The analysis was conducted using the *R* package *vegan* (Oksanen et al. 2018; https://CRAN.R-project.org/package=vegan).

Results

We identified a total of 25 syllable types and eleven song types (Fig. 1c, 3). The intraobserver repeatability analysis produced a high intraclass correlation coefficient (ICC = 0.898, 95% CI 0.883–0.911), indicating consistent syllable type designations. The most common song types, 1, 4, and 6, were sung by 55% (16/29) of males and were spatially clustered, a pattern suggestive of song neighborhoods (Fig. 1b). The hierarchical cluster analysis showed that songtypes 6, 7, and 10 were similar in syllable use, as were songtypes 1, 2, and 9 (Fig. 1a). These relationships among groups of songtypes were largely consistent with the spatial distributions of the different songtypes (Fig. 1b), such that the territories of males that share many syllable types tend to be spatially clustered.

The majority of syllable type diversity was found in phrases A and B (Fig. 3). Consistent with the results of the hierarchical cluster analysis, we found a significant positive relationship between physical distances between males and syllable use distances (Fig. 4a; Mantel, $r = 0.32$, $r^2 = 0.108$, $p < 0.0001$). In contrast, there was no relationship between physical distance and song distance derived from spectral and temporal measures (Fig. 4b; Mantel, $r = 0.056$, $r^2 = 0.0031$, $p = 0.328$).

We found little overlap between syllable types identified in 2021 and earlier time points. Specifically, of the eight A syllable types found in the 1980's, only two were found in 2021. Likewise, of the eleven syllable types identified in phrases B and C from earlier recordings, only one (the

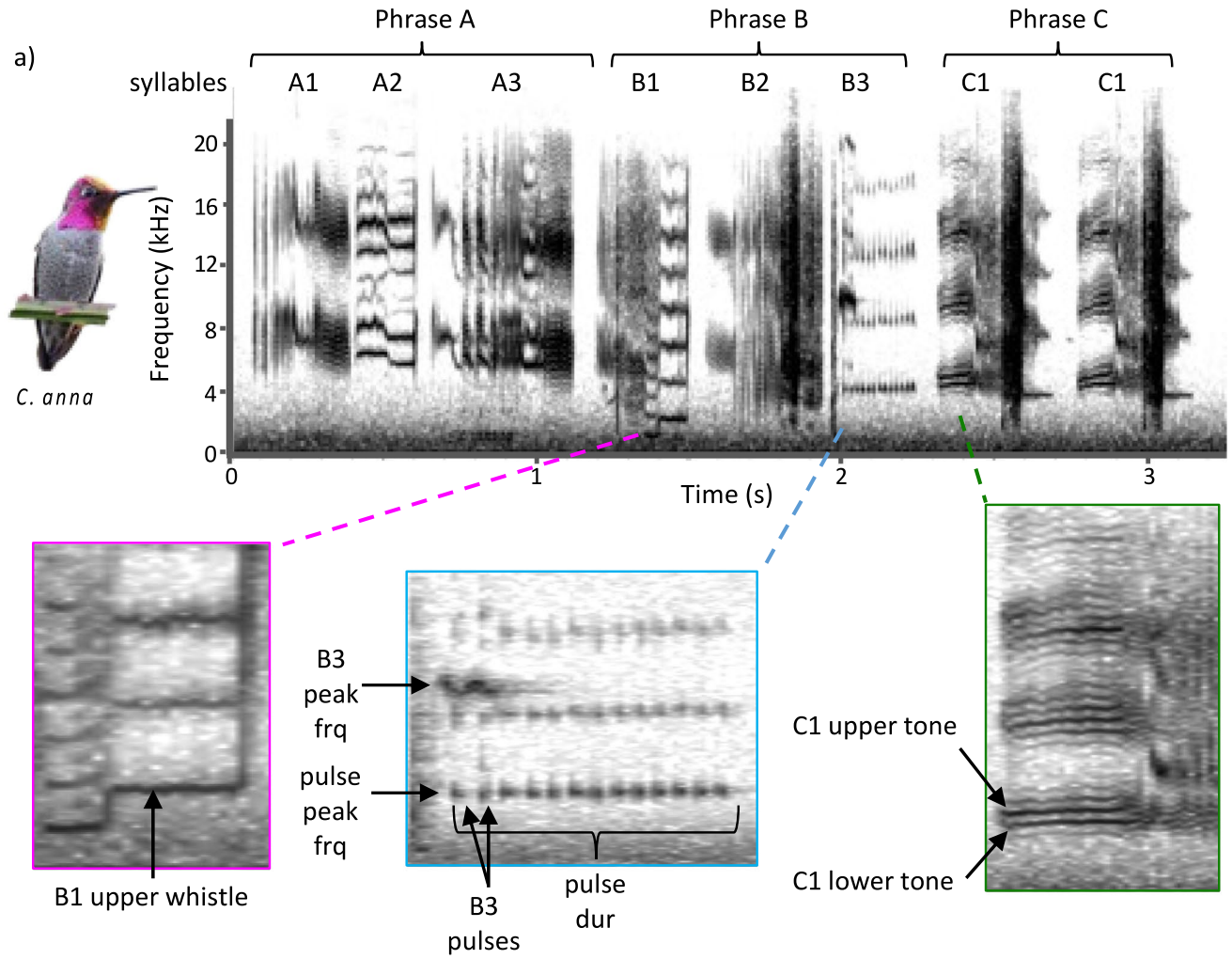


Fig. 2 Anna's Hummingbird (*Calypte anna*) song and spectral and temporal measurements. Anna's hummingbirds sing a complex three phrase (**A**–**C**) song with multiple syllables (A1–A3, B1–B3, C1). Peak frequency and duration was taken for full syllables (A1–C1), and for each of the highlighted elements (B1 upper whistle, B3 pulses, C1 upper tone, and C1 lower tone); pulse number and rate were measured for B3. Image, Steven Mlodinow

conserved C1 syllable, equivalent to syllable 'Db' in Yang et al. 2007) was found in 2021 (Fig. 3). In 1985, 1987, and 1999 songs, phrase B consisted of two main syllables whereas in 2021 the second B syllable ('Zwee' in Yang et al. 2007) was split in two, with a gap between syllable B2 and B3 and a broadband click marking the start of syllable B3 in all songs (Fig. 5).

Overall, we identified fewer syllable types than did Yang and colleagues in 1999 (25 vs. 38). However, Yang and colleagues' inclusion of nine birds from two other populations around 5 km and around 20 km from Golden Gate Park may have contributed to their higher syllable type count. Using the Lomolino model, we projected that the rarefaction curve for 2021 syllable types would asymptote at 30.1, suggesting that we sampled the majority (83.1%) of current variants in the population (Fig. 6). Using the same model, we projected that the rarefaction curve for the recordings from the 1980's would asymptote at 25.7, suggesting that the archived recordings sampled 76.9% of the total syllable types in the population at that time. Accumulation curves for 2021 and 1980's syllable types are provided in electronic supplementary material Fig. 2.

Discussion

Anna's Hummingbird males have complex learned songs that are sung from breeding territories during the species' breeding season from January to June. We sampled male songs from a single breeding population in Golden Gate Park with the goals of cataloguing acoustic diversity and

Table 1 Spectral and temporal measures of Anna's hummingbird (*Calypte anna*) song

	Measurements
Phrase A	A1 Duration (seconds)
A1	A1 Peak frequency (kHz)
A2	A2 Duration (seconds)
A3	A2 Peak frequency (kHz)
	A3 Duration (seconds)
	A3 Peak frequency (kHz)
Phrase B	B1 Peak frequency (kHz)
B1	B1 Duration (seconds)
B2	Upper whistle Peak frequency (kHz)
B3	B2 Peak frequency (kHz)
	B2 Duration (seconds)
	B3 Peak frequency (kHz)
	B3 Duration (seconds)
	Peak frequency pulses (kHz)
	Duration pulses (seconds)
	Number of pulses (#)
	Pulse rate (# pulses/second)
Phrase C	Peak frequency (kHz)
C1	Duration (seconds)
	Peak frequency lower tone (kHz)
	Duration lower tone (seconds)
	Peak frequency upper tone (kHz)
	Duration upper tone (seconds)

evaluating spatial and temporal effects on acoustic variation. We identified 25 syllables and eleven song types, and found that both were affected by inter-male distances, such that males with adjacent territories were more similar in syllable and song type usage than were males with more distant territories (Fig. 1, 4a). We found no such relationship for spectral and temporal measures of song (Fig. 4b). The turnover of syllable types between the 1980's and 2021 in Golden Gate Park is indicative of rapid cultural evolution of song in a single population. We consider the potential function and social mechanism of song sharing in Anna's, and discuss evidence for contrasting patterns of rapid cultural evolution and stability of Anna's song.

Why and how do male Anna's learn their neighbors' songs?

Song sharing has proposed adaptive functions in territorial defense (Krebs et al. 1981; Stoddard et al. 1991; Stoddard 1996) and reproduction (Payne 1982; Payne et al. 1988). Shared song types may, for example, facilitate neighbor recognition, allowing reduced aggression between neighbors holding established territories (the 'dear enemy' effect; Fisher 1954; Temeles 1994; Jaška et al. 2015). Similarly, in flock-forming parrots, rapid vocal convergence with novel interaction partners is thought to facilitate integration into transient social groups (Balsby and Bradbury 2009; Scarl and Bradbury 2009). However, in territorial songbirds with repertoires of song types and syllables, counter-singing matched song types can also serve to indicate threat and escalate agonistic interactions (Bertram 1970; Beecher et al. 2000; Anderson et al. 2005; Beecher and Campbell 2005).

Anna's Hummingbirds are extremely aggressive and territorial and engage in frequent high-speed chases with conspecific males and other sympatric hummingbird species (Pitelka 1951). These chases often are accompanied by singing and males will display to all intruders that enter their territories, including other species and male conspecifics (Stiles 1982). We hypothesize that sharing song types with neighbors decreases the number of agonistic interactions between males on neighboring breeding territories. Testing this hypothesis will require playback experiments to determine whether shared and non-shared song types elicit different levels of aggressive response.

The effect size of spatial distance on song distance ($r^2 = 0.108$; Fig. 4a) is small but comparable in magnitude to effect sizes found in similar studies of oscine species (Mantel $r^2 = -0.171$; Koetz et al. 2007) and hummingbirds (Mantel $r^2 = 0.24$; Araya-Salas et al. 2019). Substantial variation around the best fit line indicates that patterns of song sharing between Anna's males are not fully explained by straight-line distances between their territories. The fact that appropriate habitat for territories and feeding are not evenly distributed in the park likely contributes. Individuals that lack food sources on their territory must leave their territories to feed, sometimes flying miles to forage (Powers 1987). Thus, conflict between conspecific males that are not territory neighbors is likely common. In these contexts, individuals hear other song types and thus song-sharing patterns might also be affected by song learning that occurs off-territory.

Song sharing is a result of song learning – the social process in which a young bird hears and memorizes a song template from an adult conspecific, practices singing to match their memorized template, and then crystalizes a song form (Marler and Slabbekoorn 2004). Birds have diverse song learning timelines that are broadly categorized as closed- or open-ended. Closed-ended song learners are classified as birds whose song repertoire is fixed by the end of their first year whereas open-ended song learners can add new variants and embellishments, including the songs of their neighbors, to their repertoire later in life (Lemon 1968; McGregor and Krebs 1989; Beecher and Brenowitz 2005). The conditions under which song sharing can occur in closed-ended learners are more restrictive. Young males must either memorize multiple song types pre-dispersal and retain those that match their neighbors' on breeding territories, or learn songs and hold territories in the same location (Beecher et al. 1997; Payne 1997; MacGregor and Krebs 1989; Nelson 2000).

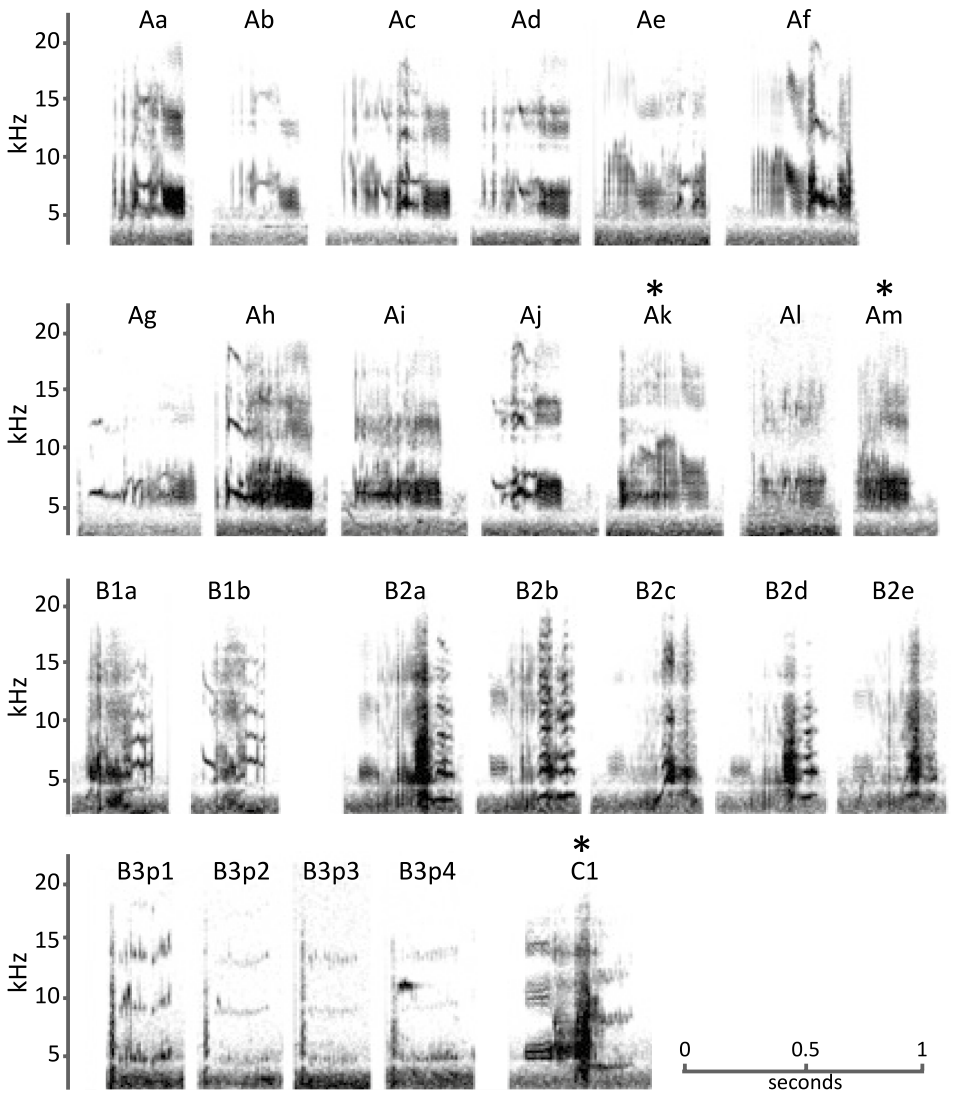


Fig. 3 Anna's Hummingbird (*Calypte anna*) syllable types. Twenty-five syllable types were identified among 29 individuals sampled in 2021. * indicates syllable types that exist in recordings from the 1980's

In hummingbirds, open-ended learning is well supported in the Long-billed Hermit (Araya-Salas and Wright 2013) and in Costa's Hummingbird (*Calypte costae*; Johnson and Clark 2022, 2024), the sister species to Anna's. An experiment conducted with a single male Anna's reared in acoustic isolation and exposed to conspecific song as an adult (Baptista and Schuchmann 1990) is suggestive of closed-ended learning as the male did not modify his incomplete song to match that of his tutor. However, because the period of exposure was brief (one month), the potential for seasonal variation in male Anna's capacity to modify song was not taken into account (Baptista and Schuchmann 1990). Moreover, acoustic isolation during the stage when song templates are initially formed might disable the capacity to modify song in later life (Chaiken and Bohner 2007). Thus, a more complete understanding of the social mechanism of song sharing in Anna's awaits long term studies of the ontogeny and social context of song acquisition in this species. Moreover, combining acoustic analyses with genotypic estimates of relatedness would help to determine the relative influence of fathers vs. neighbors on song learning in Anna's.

Because song is used in female directed courtship displays and because Anna's are polygynous, it is likely that song is shaped by female preference. However, whether and how female preference shapes microgeographic patterns of song sharing is unclear. Further research on female song preference and mate choice is needed in Anna's hummingbirds.

Contrasting patterns of lability and stability in Anna's song

We found differences in the rate of cultural evolution in Anna's song, both across time periods and within the song

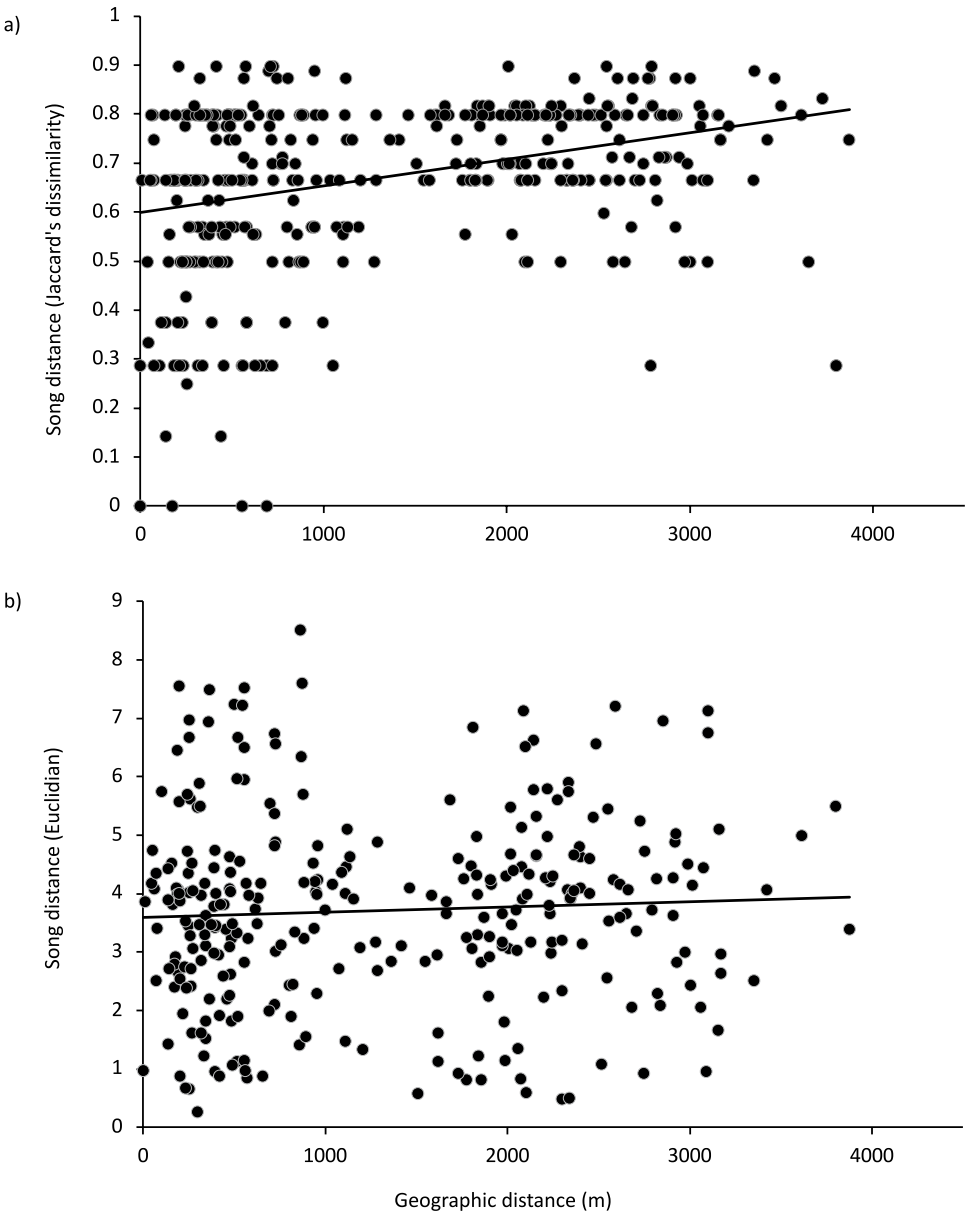


Fig. 4 Effect of physical distance on song distance in Anna's Hummingbird (*Calypte anna*) for **a** syllable use (Mantel, $r = 0.32$, $r^2 = 0.108$, $p < 0.0001$) and **b** spectral and temporal components (Mantel, $r = 0.056$, $r^2 = 0.0031$, $p = 0.328$). Physical distance calculated as linear distance in meters between each individual. Song distance for syllable use calculated as Jaccard distance; song distance for spectral and temporal components calculated as Euclidian distance. Each point represents a contrast between two of the 29 birds recorded ($n = 406$ contrasts)

itself. Neither syllable stability nor high rates of turnover are surprising; both patterns are common in longitudinal studies of oscine birdsong (e.g. Payne 1985; Sorjonen 1987; Trainer 1983; Harbison et al. 1999). However, why the rate of cultural evolution of song should be different across comparable time periods (twelve and 22 years) is unclear. As a large protected green space in an urban area, we would expect the biotic and acoustic environment of Golden Gate Park to be stable over recent decades.

We found substantial change in the structure of phrase B. Whereas all males recorded in 1985, 1987, and 1999 had two syllables in phrase B, all birds recorded in 2021 had three. The third syllable in phrase B (B3) shares characteristics with the end of phrase B in the earlier recordings but begins with a broadband note and a clear inter-syllable gap. Interestingly, this change to phrase B in the Golden Gate Park Anna's population is ubiquitous in recordings collected during the 2020 and 2021 breeding seasons from five other populations across the Western United States (Berger et al. 2025). If the structural change to phrase B arose after 1999, such rapid spread of the new three-syllable variant would require strong positive selection, perhaps due to female preference. Alternatively, the two-syllable phrase B from earlier recordings at Golden Gate Park was a local variant that disappeared from that population some time after 1999. Discriminating between these possibilities would require evaluation of the structure of phrase B in earlier recordings from populations across the species' range.

Interestingly, birds from all three time points sang the same version of syllable C1. The stability of C1 relative to

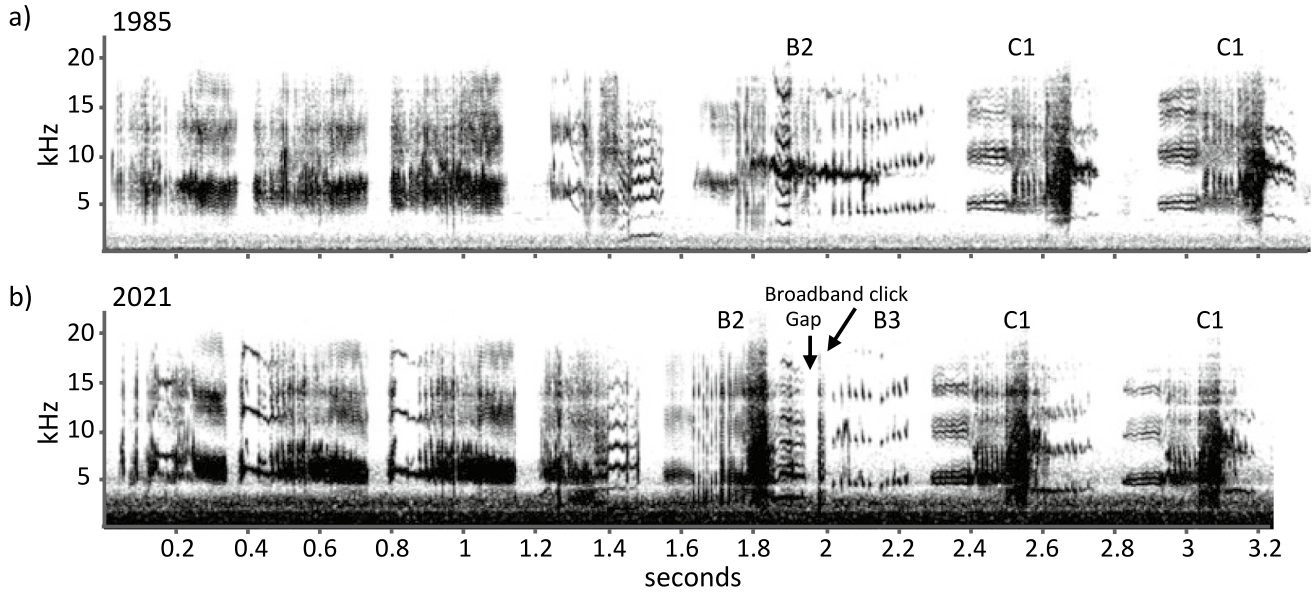


Fig. 5 Representative spectrograms for Anna's Hummingbird (*Calypte anna*) song recorded in **a** 1985 and **b** 2021. A gap between syllables B2 and B3 and a broadband click are present in 2021 songs only. The 1985 song was recorded by LF Baptista and K-L Schuchmann and retrieved from the Borror Laboratory of Bioacoustics (BLB34883; blb.osu.edu/database/; The Ohio State University). The 2021 song can be found on Xeno-Canto at XC958868

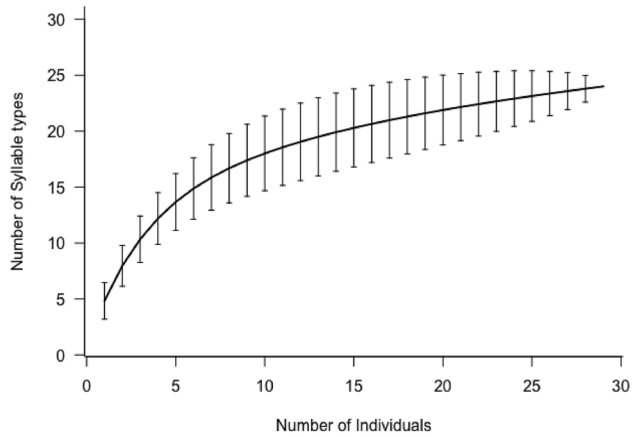


Fig. 6 Rarefaction curve of the number of syllable types for 29 Anna's Hummingbirds (*Calypte anna*). The Lomolino model projects an asymptote at 30.1 individuals. 95% Confidence Intervals indicated by the vertical lines

the rest of the song is indicative of a constraint on variation. Whereas Yang et al. (2007) found six C syllable types, we found only one, suggesting reduction in variation over time. In some species, songs are hypothesized to segregate into elements containing information of varying specificity, such as individual, population, or species identity (Marler 1960; Brenowitz 1982; Elfström 1990; Nelson and Poesel 2007). Individual identity signals have high intraspecific variation in both song form and fine temporal structure (Katharina and Nieder 2020; Pruchová et al. 2017; Prior et al. 2018), whereas signals of species or population identity have less variation and are less labile (Marler 1960). For example, in White-crowned Sparrows (*Zonotrichia leucophrys*), introductory whistles did not vary geographically as compared to the other phrases in the song and were stable over a 30-year period (Harbison et al. 1999; Nelson and Poesel 2007). In our study, the high diversity and turnover of A syllables and the structural change in B syllables suggest that the first part of the song encodes individual or song neighborhood identity. In contrast, the low diversity of phrase C, especially in 2021, suggests that this phrase encodes species identity. Yang et al. (2007) proposed that syllable type sharing indicates that song is learned on a syllable level. However, the observation of a limited number of song types suggests learning at the song level. Playback experiments that modify each syllable will help to determine the social functions of syllable variation, stability, and sharing in Anna's Hummingbird. Song learning experiments could also elucidate how Anna's learn their songs by testing whether song is learned syllable by syllable, or songtype by songtype.

Conclusion

Our results suggest some level of song sharing among neighbors in the territorial song learning Anna's Hummingbird. We show that common song types are loosely organized into song neighborhoods and that syllable

sharing decreases with distance between territories. We find evidence for high syllable turnover in the first and most variable phrase of Anna's song, and contrasting stability in the terminal phrase. These results motivate future work on the function of song sharing in Anna's and the information content of the species' multi-phrase song. As a species with a complex song that is invariant within individual, Anna's is just one of over 300 hummingbird species whose diverse vocalizations range from no song, to simple songs, to large individual repertoires of complex songs (Monte et al. 2023). Such diversity of learned song makes hummingbirds a fascinating clade for comparative analysis of the evolution of song structure and complexity.

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Data availability Sound recordings from this study are publicly available on Xeno-Canto (https://xeno-canto.org/). Catalogue IDs for this study are available as electronic supplementary material Table S1.

Declarations

Conflcit of interest The authors declare no conflicts of interest.

Ethical approval All work was done in accordance with UCR IACUC protocols 20160039 and 20190019. Hummingbirds were recorded in the field from a minimally disruptive distance and generally out of sight of the focal birds.

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