Seasonal song variation in male Carolina Wrens (*Thryothorus ludovicianus*)

Holly R. Keating¹ and Dustin G. Reichard^{1*}

¹Ohio Wesleyan University, Department of Zoology, 61 S Sandusky St, Delaware, OH 40315

*Corresponding Author email: dgreicha@owu.edu; 740-368-2890

ABSTRACT—Birdsong’s primary function is attracting and stimulating mates and repelling rivals during the breeding season. However, many species also sing during the nonbreeding season, which raises questions about the function of nonbreeding song and the proximate mechanisms underlying its production. In this study, we compared spectral and temporal measurements from a large sample of breeding ($N = 267$) and nonbreeding songs ($N = 283$) of Carolina Wrens (*Thryothorus ludovicianus*), a nonmigratory, temperate species that sings year-round. We found that breeding songs were longer than nonbreeding songs and had more syllables within each song. Trill rate, the number of notes per syllable, minimum and maximum frequency and frequency bandwidth did not differ detectably between the two seasons. This study is the first to examine seasonal song differences in Carolina Wrens and provides a basis for future investigations into the drivers behind this seasonal variation.

Key words: seasonal variation, song length, territoriality, songbird, annual cycle, bioacoustics, wren

The majority of research on avian vocal behavior has focused on male songs during the breeding season in north temperate climates (Catchpole and Slater 2008). This bias has led to the assumption that most songbirds primarily sing to attract mates and repel rivals during breeding with songs being replaced by calls or silence for the remainder of the year. However, many species of both temperate and tropical songbirds are known to sing outside the breeding season (reviewed in Gahr 2020), including migratory species that sing on their wintering grounds (Sorensen et al. 2016). Despite the abundance of nonbreeding songs, the seasonality of song production and structure has been studied quantitatively in very few species. In those species that have been studied, seasonal changes in song complexity and structure such as song length, syllable repetition rates, syllable consistency, and repertoire composition are inconsistent and species specific (Gahr 2020). Expanding our focus to nonbreeding songs will provide a more complete understanding of the proximate mechanisms underlying song production as well as the full array of functions that songs might serve.

Carolina Wrens (*Thryothorus ludovicianus*) are nonmigratory songbirds found across the eastern United States and Mexico that sing during the breeding and nonbreeding seasons (Fig. 1). Unlike most temperate songbirds, Carolina Wrens form long-term pair bonds and both members of the pair engage in territorial defense year-round (Morton and Shalter 1977, Haggerty et al. 2001). Only males sing, and each individual produces a repertoire of 17-55 (mean = 32) unique song types (Fig. 1; Morton 1987). Song functions in territorial behavior, but song production seems to increase at the onset of the breeding season, suggesting an additional function in courtship and mate stimulation (Haggerty and Morton 2020). A function in mate attraction is less clear given that pair bonds can form in the first few months of life before males fully develop a

crystallized song (Morton 1982). Despite this persistent vocal behavior, seasonal variation in the structure of Carolina Wren song has yet to be quantified.

In this study, we compared breeding and nonbreeding Carolina Wren songs across a large geographic scale using recordings from online databases. We hypothesized that songs would differ between the breeding and nonbreeding seasons. Specifically, we predicted that breeding season songs would be longer and more complex (more notes/syllable, higher entropy) due to song's presumed function in courtship and mate stimulation during breeding. In addition, nonbreeding songs may be shorter and less complex due to seasonal reductions in the size of brain nuclei responsible for song production even in species that sing all year (Smith et al. 1995, 1997; but see Leitner et al. 2001, Smulders 2005).

Methods

Song Recordings

We obtained recordings of Carolina Wren (*Thryothorus ludovicianus*) songs from the Florida Museum of Natural History (N = 49; WAV format), xeno-canto (N = 124; MP3 format; <https://www.xeno-canto.org/>), and the Macaulay Library (N = 377; WAV format; <https://www.macaulaylibrary.org>; see Supplementary Table S1). The recordings were collected between 1954-2020 throughout the Carolina Wren's range in Canada, the United States, and Mexico (Supplementary Table S1). We inspected each recording for accuracy and quality (signal-to-noise ratio). After removing misidentified and low-quality recordings, we cross referenced the metadata for each recording to remove duplicate songs that may have been uploaded to multiple databases. We also scrutinized the recording dates and locations to prevent

the same song type from the same individual from being sampled more than once. A total of 550 unique songs were included in our analysis.

Based on the breeding phenology of Carolina Wrens (Haggerty and Morton 2020), the breeding season encompasses March to August ($N = 267$) and the nonbreeding season is September to February ($N = 283$). In the southern United States, egg laying begins in mid-March and ceases by mid-August, but pairs can continue to feed young as late as early October (Haggerty and Morton 2020). To ensure that our results were not skewed by samples from the transitional months between breeding and nonbreeding, we ran an identical analysis that excluded all recordings collected in February and September ($N = 106$ songs excluded). The results of this analysis were qualitatively identical to our complete analysis included below (Table 1, Supplementary Table S2).

Song Measurements

We used Raven Pro 1.6 (Center for Conservation Bioacoustics, 2011) to measure song length, minimum and maximum frequency, frequency bandwidth, the number of inflection points, maximum entropy, and trill rate. A single observer (HRK) analyzed all songs and was blind to breeding season. We generated spectrograms of each recording (Hann Window, 512 DFT, 93.8 Hz frequency resolution), and used the band limited energy detector to locate high quality songs. Then we randomly chose one song from each recording for analysis.

To minimize human bias, the start and end time for each song was determined by the energy detector, and we used the peak frequency contour function to measure the minimum and maximum frequency and the number of inflection points. The peak frequency contour function traces the peak frequency of a vocalization by measuring individual spectrogram slices through

time, which allows for automatic, less biased spectral measurements. The number of inflection points is calculated as the number of times the slope of the peak frequency contour changes signs across the entire song. Maximum entropy was calculated automatically.

We manually counted the number of syllables and notes per syllable for each song and trill rate was calculated as the number of syllables divided by song length. In a few cases ($N = 30$), the energy detector was unable to recognize songs in the recording despite a strong signal-to-noise ratio. When this occurred, we manually determined the start and end time by visually drawing a selection box around the song before collecting the remaining measurements with the peak frequency contour function.

Statistical Analysis

We conducted linear mixed models using the ‘lme4’ package in R v 4.0.2 (Bates et al. 2015; R Core Team, 2020) to compare breeding and nonbreeding songs. We used model selection by Akaike’s Information Criterion to assess the relative importance of latitude and sampling year as explanatory variables. For each song measurement, a series of models were created that contained the song measurement as the response variable, breeding status as a random factor, and latitude, sampling year, or both as independent factors. The models that included latitude alone were the only models to outperform the null model. We used a likelihood ratio test (LRT) to assess significance by comparing the likelihood of the full model that included latitude to that of a reduced model without breeding season.

Results

Breeding male Carolina Wrens sang longer songs than non-breeding wrens (Table 1, Fig. 2, $X^2_1 = 18.65$, $P < 0.001$) and had more syllables within each song (Table 1, Fig. 2, $X^2_1 = 11.90$, $P < 0.001$). There was no difference between breeding and nonbreeding songs in minimum or maximum frequency, frequency bandwidth, the number of notes per syllable, trill rate, the number of inflection points within a song, or maximum entropy (Table 1).

Discussion

Male Carolina Wrens sang longer songs with more syllables during the breeding season. This result was consistent with our predictions as well as previous seasonal comparisons from other species including both residents (e.g. Nuttall's White-crowned Sparrows [*Zonotrichia leucophrys nuttalli*], Brenowitz et al. 1998; Wild Canaries [*Serinus canaria*], Leitner et al. 2001; Black-Capped Chickadees [*Poecile atricapillus*], Smulders 2005; Rufous-capped Warblers [*Basileuterus rufifrons*], Demko and Mennill 2019) and migrants (Gambel's White-crowned Sparrows [*Zonotrichia leucophrys gambelii*], Smith et al. 1995). However, we found no detectable seasonal differences in trill rate, the number of notes per syllable, number of inflection points, maximum entropy, or any measures of frequency. This outcome indicates that Carolina Wrens are singing similarly structured songs throughout the year rather than producing more complex songs during the breeding season as we predicted. One limitation of this study was that we were unable to compare the song repertoires of individual males between the breeding and nonbreeding seasons, so it remains unknown whether repertoire composition or the stereotypy of individual song types vary seasonally, which has been observed in other species (Smith et al. 1997, Leitner et al. 2001).

The relative lack of seasonal variation in Carolina Wren song structure may be partially explained by the primary function of song in this species. As a temperate resident, Carolina Wrens defend territories year-round, and a persistent function of song appears to be in territorial behavior (Haggerty and Morton 2020). Maintaining a viable territory is not only important for breeding, but nonbreeding territories are critical for overwinter survival in this species, particularly during harsh winters when food resources become scarce and adult mortality can reach 90% (Morton 1982). This intense nonbreeding territoriality is further supported by the fact that Carolina Wrens ignore dear-enemy effects and engage in more territorial disputes during the nonbreeding season, and males with higher quality territories during harsh winters sing at higher rates than males with low quality territories (Morton and Shalter 1977, Morton 1982, Hyman 2005). Additionally, unpaired females, which do not sing, are unable to maintain territories alone, but solo males can (Morton and Shalter 1977). Collectively, these observations suggest that song's year-round role in territoriality may be the most important selective force maintaining its consistent structure across the breeding and nonbreeding seasons.

Unlike many temperate songbirds, Carolina Wrens form long term pair bonds that are often established early in life before males develop a crystalized song (Morton and Shalter 1977). Under these conditions, females likely choose mates based on a male's non-vocal attributes or the quality of his territory, which minimizes the traditional function of song in mate attraction. The presence of long-term genetic monogamy in Carolina Wrens (Haggerty et al. 2001) also makes it unlikely that song functions in attracting extra-pair mates. However, male wrens increase their song rates at the beginning of breeding (Haggerty and Morton 2020), and our study supports a concurrent increase in song length and the number of repetitions of each syllable during the breeding season. Increasing song length and redundancy can increase the

detectability of the signal for all potential receivers, which would support functions in both inter and intrasexual communication during breeding (Price 2013). Independent of mate attraction, longer breeding songs may also function in within-pair communication as a contact signal (Baptista 1978) and in stimulating females into reproductive condition (Maney et al. 2007).

The underlying mechanism for the seasonal changes in song length could be due to a variety of factors, including changes in brain nuclei size or shifting hormonal controls. Multiple species of sparrows have divergent song structures in the fall when song control nuclei are significantly smaller (Smith et al 1995, 1997; Brenowitz et al. 1998), but other species such as Black-Capped Chickadees sing longer songs during the breeding season with no seasonal variation in the size of the song system nuclei (Smulders 2005). Male Carolina Wrens have larger song control nuclei than females (Nealen and Perkel 2000), but whether the size of these nuclei vary seasonally is unknown and represents an important topic for future research. Alternatively, changes in sex steroid concentrations or receptor densities and locations could cause seasonal song differences and may or may not work in conjunction with changes in brain nuclei size. Wild canaries, for example, produce longer songs with faster trill rates during the breeding season when plasma testosterone levels are significantly higher, but the size of at least two song system nuclei remains similar between breeding and nonbreeding (Leitner et al. 2001, Voigt and Leitner 2008). Elevated androgen levels appear to consistently increase song rates in seasonally breeding species, but the exact role of androgens in determining song structure, particularly during the nonbreeding season when plasma levels are often low, remains poorly understood (reviewed in Gahr 2020).

The majority of our assumptions about the ultimate and proximate mechanisms underlying birdsong structure and function are derived from studies of breeding songs in

temperature species. Nonbreeding songs are common, and their production is often regulated by mechanisms that cannot be easily explained by circulating levels of sex steroids (Gahr 2020). Songs produced outside the breeding season are also more likely shaped by functions in territoriality and competition rather than mate attraction and choice. Expanding our focus to species such as Carolina Wrens, which sing throughout the year, may provide new insights into the mechanisms of song production and the complexity of selective forces that shape song structure.

Acknowledgments

We thank the Macaulay Library at the Cornell Lab of Ornithology, xeno-canto, and the Florida Museum of Natural History for use of their song recordings. We thank the Ohio Wesleyan University Summer Science Research Program for funding.

Literature Cited

- Baptista LF. 1978. Territorial, courtship and duet songs of the Cuban Grassquit (*Tiaris canora*). Journal für Ornithologie. 119:91-101.
- Bates DM, Mächler M, Bolker BM, Walker S. 2015. Package lme4: Linear mixed-effects models using Eigen and S4. Journal of Statistical Software. 67:1-48.
- Brenowitz,EA, Baptista LF, Lent K, Wingfield JC. 1998. Seasonal plasticity of the song control system in wild Nuttall's White-crowned Sparrows. Journal of Neurobiology. 34:69-82.
- Catchpole CK, Slater PJB. 2008. Bird Song: Biological Themes and Variations. Cambridge University Press, Cambridge.

Center for Conservation Bioacoustics. 2011. Raven Pro: Interactive sound analysis software.
Version 1.6. Ithaca, NY: Cornell Lab of Ornithology. Available from:
<http://ravensoundsoftware.com/>.

Demko AD, Mennill, DJ. 2019. Rufous-Capped Warblers *Basileuterus Rufifrons* show seasonal, temporal and annual variation in song use. *Ibis*. 161:481–94.

Gahr, M. 2020. Seasonal Hormone Fluctuations and Song Structure of Birds. In *Coding Strategies in Vertebrate Acoustic Communication*, edited by Thierry Aubin and Nicolas Mathevon, 7:163–201.

Haggerty TM, Morton ES, Fleischer RC. 2001. Genetic Monogamy in Carolina Wrens (*Thryothorus ludovicianus*). *Auk*. 118:215–219.

Haggerty TM, Morton ES. 2020. Carolina Wren (*Thryothorus ludovicianus*). In: Poole AF, editor. *Birds of the World*. Ithaca (NY): Cornell Laboratory of Ornithology.
<https://doi.org/10.2173/bow.carwre.01>

Hyman, J. 2005. Seasonal variation in response to neighbors and strangers by a territorial songbird. *Ethology*. 111:951-961.

Leitner S, Voigt C, Garcia-Segura LM, Van't Hof T, Gahr M. 2001. Seasonal activation and inactivation of song motor memories in wild canaries is not reflected in neuroanatomical changes of forebrain song areas. *Hormones and Behavior*. 40:160–168.

Maney DL, Goode CT, Lake JJ, Lange HS, O'Brien S. 2007. Rapid neuroendocrine responses to auditory courtship signals. *Endocrinology*. 148:5614-5623.

Morton, ES, Shalter. MD. 1977. Vocal response to predators in pair-bonded Carolina Wrens. *Condor*. 79:222-227.

Morton, ES. 1982. "Grading, discreteness, redundancy, and motivation-structural rules." In
Acoustic communication in birds, edited by D. E. Kroodsma and E. H. Miller, 183-212.

Morton, ES. 1987. The effects of distance and isolation on song-type sharing in the Carolina
Wren. *Wilson Bulletin*. 99:601-610.

Nealen, PM and Perkel, DJ. 2000. Sexual dimorphism in the song system of the Carolina Wren
Thryothorus ludovicianus. *Journal of Comparative Neurology*. 418:346-360.

Price, JJ. 2013. Why is birdsong so repetitive? Signal detection and the evolution of avian
singing modes. *Behavior*. 2013:995-1013.

R Core Team. 2020. R: A language and environment for statistical computing. Vienna, Austria:
R Foundation for Statistical Computing. <https://www.R-project.org/>.

Smith, G. Troy, Eliot A. Brenowitz, John C. Wingfield, Luis F. Baptista. 1995. Seasonal
changes in song nuclei and song behavior in Gambel's White-Crowned Sparrows.
Journal of Neurobiology. 28:114-125.

Smith G, Troy EA, Brenowitz MD, Beecher, Wingfield, JC. 1997. Seasonal changes in
testosterone, neural attributes of song control nuclei, and song structure in wild
songbirds. *The Journal of Neuroscience*. 17:6001–6010.

Smulders TV, Lisi ME, Tricomi E, Otter KA, Chruszcz B, Ratcliffe LM, DeVoogd TJ. 2006.
Failure to detect seasonal changes in the song system nuclei of the Black-Capped
Chickadee (*Poecile atricapillus*). *Journal of Neurobiology*. 66:991–1001.

Sorensen MC, Jenni-Eiermann S, Spottiswoode CN. 2016. Why do migratory birds sing on their
tropical wintering grounds? *American Naturalist*. 187:E65–E76.

Voigt C, Leitner, S. 2008. Seasonality in song behaviour revisited: seasonal and annual variants and invariants in the song of the Domesticated Canary (*Serinus Canaria*). Hormones and Behavior. 54:373–378.

Figure Captions

Figure 1. Representative spectrograms of Carolina Wren songs from the breeding (top) and nonbreeding (bottom) seasons. The darkness of the spectrograms does not represent the relative amplitudes of the songs.

Figure 2. Comparison of song measurements from Carolina Wrens that showed a significant difference between breeding and nonbreeding seasons. Each box represents the interquartile range and median, whiskers represent range of data within 1.5 times the interquartile range, and dots represent data points exceeding that range. $*P < 0.01$

Table 1. Results of linear mixed model analysis for song measurements comparing breeding and nonbreeding populations. All means are presented $\pm$ 1 SEM. Bolded values identify $P < 0.05$.

Song Measurement	Breeding Mean	Nonbreeding Mean	χ^2_{df}	P -value
Song Length (sec)	1.69$\pm$0.02	1.56$\pm$0.02	18.77	< 0.001
Maximum Frequency (Hz)	5483.0 $\pm$ 61.24	5453.8 $\pm$ 59.51	0.07	0.79
Minimum Frequency (Hz)	1788.9 $\pm$ 16.68	1828.1 $\pm$ 17.71	2.06	0.15
Frequency Bandwidth (Hz)	3694.03 $\pm$ 62.22	3625.70 $\pm$ 60.38	0.31	0.58
Number of Inflection Points	94.96 $\pm$ 1.72	97.95 $\pm$ 1.91	0.01	0.92
Maximum Entropy	4.90 $\pm$ 0.02	4.85 $\pm$ 0.03	1.43	0.23
Number of Syllables/Song	4.78$\pm$0.09	4.26$\pm$0.08	11.9	< 0.01
Number of Notes/Syllable	4.86 $\pm$ 0.07	4.92 $\pm$ 0.07	0.006	0.94
Trill Rate (syllables/sec)	2.79 $\pm$ 0.06	2.76 $\pm$ 0.05	0.06	0.8

Figure 1

Figure 2

322 **Supplementary Table S1.** Reference information for the recordings obtained from online
323 databases.

Database Name	Recording Identification Number	Date of Recording	Recordist Name
Macaulay Library	9086	2/12/1954	Arthur A. Allen
Macaulay Library	9088	4/26/1955	Peter Paul Kellogg
Macaulay Library	9089	4/27/1955	Peter Paul Kellogg
Macaulay Library	9093	4/24/1961	Robert C. Stein
Macaulay Library	9094	3/25/1962	Randolph Little
Macaulay Library	9095	3/28/1962	Randolph Little
Macaulay Library	9096	3/30/1962	Randolph Little
Macaulay Library	9097	6/9/1962	James Kimball
Macaulay Library	9098	6/11/1962	James Kimball
Macaulay Library	9099	5/1/1960	Marian P. McChesney
Macaulay Library	9200	4/17/1963	Robert C. Stein
Macaulay Library	9201	4/18/1963	Robert C. Stein
Macaulay Library	9203	4/28/1963	Robert C. Stein
Macaulay Library	9204	4/30/1963	Robert C. Stein
Macaulay Library	9205	5/2/1963	Robert C. Stein
Macaulay Library	9206	5/7/1963	Robert C. Stein

Macaulay Library	9208	4/27/1964	Marian P. McChesney
Macaulay Library	9210	4/14/1964	Marian P. McChesney
Macaulay Library	9215	4/26/1964	Randolph Little
Macaulay Library	9216	5/10/1964	Randolph Little
Macaulay Library	9217	3/19/1970	Marian P. McChesney
Macaulay Library	9219	7/21/1970	James Kimball
Macaulay Library	9220	6/9/1962	James Kimball
Macaulay Library	14665	5/5/1960	Peter Paul Kellogg
Macaulay Library	26401	3/18/1979	Randolph Little
Macaulay Library	26796	3/31/1980	Margery R. Plymire
Macaulay Library	30296	5/3/1975	Randolph Little
Macaulay Library	37351	5/3/1986	Geoffrey A. Keller
Macaulay Library	37355	5/3/1986	Geoffrey A. Keller
Macaulay Library	37370	5/4/1986	Geoffrey A. Keller
Macaulay Library	38330	3/26/1986	Ted Parker
Macaulay Library	40788	5/7/1988	Gregory Budney
Macaulay Library	41373	3/5/1983	Dolly Minis
Macaulay Library	41375	3/9/1983	Dolly Minis
Macaulay Library	42394	8/9/1984	Gregory Budney
Macaulay Library	45610	6/1/1988	Ted Parker

Macaulay Library	51801	5/19/1989	Ted Parker
Macaulay Library	63232	3/3/1966	William W. H. Gunn
Macaulay Library	72274	4/24/1992	Geoffrey A. Keller
Macaulay Library	73999	4/24/1992	Geoffrey A. Keller
Macaulay Library	74003	4/24/1992	Geoffrey A. Keller
Macaulay Library	77268	3/2/1996	Wil Hershberger
Macaulay Library	84682	2/16/1997	Wil Hershberger
Macaulay Library	84703	2/28/1997	Wil Hershberger
Macaulay Library	100722	3/17/1999	Wil Hershberger
Macaulay Library	100751	4/4/1999	Wil Hershberger
Macaulay Library	105331	5/4/1994	Geoffrey A. Keller
Macaulay Library	105372	5/10/1994	Geoffrey A. Keller
Macaulay Library	105515	4/24/1995	Geoffrey A. Keller
Macaulay Library	105559	4/30/1995	Geoffrey A. Keller
Macaulay Library	128905	3/21/2005	Gerrit Vyn
Macaulay Library	128919	3/17/2005	Gerrit Vyn
Macaulay Library	129800	3/20/2006	Randolph Little
Macaulay Library	132979	2/27/2007	Michael Andersen
Macaulay Library	135379	5/5/2005	Brian O'Shea
Macaulay Library	136203	3/13/2007	Martha Fischer

Macaulay Library	146530	3/23/2006	Mark Robbins
Macaulay Library	147823	3/18/2005	Benjamin Clock
Macaulay Library	147835	3/22/2005	Benjamin Clock
Macaulay Library	165256	8/2/2010	Hope Batcheller
Macaulay Library	172329	5/26/2011	Mark Robbins
Macaulay Library	176214	6/30/2009	Geoffrey A. Keller
Macaulay Library	183180	3/16/2014	Mary Margaret Ferraro
Macaulay Library	188894	9/16/2013	Bob McGuire
Macaulay Library	191224	7/3/2012	Wil Hershberger
Macaulay Library	196481	3/19/2011	Bob McGuire
Macaulay Library	205452	4/5/2001	Dustin Strom
Macaulay Library	213709	4/18/2008	Bob McGuire
Macaulay Library	219744	6/4/2009	Bob McGuire
Macaulay Library	225837	9/30/2009	Bob McGuire
Macaulay Library	225838	9/30/2009	Bob McGuire
Macaulay Library	225842	10/3/2009	Bob McGuire
Macaulay Library	225862	10/4/2009	Bob McGuire
Macaulay Library	225871	10/5/2009	Bob McGuire
Macaulay Library	225873	10/5/2009	Bob McGuire
Macaulay Library	225874	10/5/2009	Bob McGuire

Macaulay Library	225874	10/6/2009	Bob McGuire
Macaulay Library	225876	10/5/2009	Bob McGuire
Macaulay Library	225878	10/5/2009	Bob McGuire
Macaulay Library	225987	12/3/2009	Bob McGuire
Macaulay Library	229157	12/13/2009	Bob McGuire
Macaulay Library	514794	4/17/2013	Wil Hershberger
Macaulay Library	514795	4/19/2013	Wil Hershberger
Macaulay Library	518367	3/25/2016	Mark Robbins
Macaulay Library	539358	2/20/2018	Wil Hershberger
Macaulay Library	539360	2/26/2018	Wil Hershberger
Macaulay Library	539362	2/28/2018	Wil Hershberger
Macaulay Library	539365	3/1/2018	Wil Hershberger
Macaulay Library	539450	3/19/2018	Wil Hershberger
Macaulay Library	539579	3/24/2018	Wil Hershberger
Macaulay Library	539591	3/27/2018	Wil Hershberger
Macaulay Library	539593	3/31/2018	Wil Hershberger
Macaulay Library	539617	4/10/2018	Wil Hershberger
Macaulay Library	539635	4/19/2018	Wil Hershberger
Macaulay Library	539654	5/3/2018	Wil Hershberger
Macaulay Library	539709	5/21/2018	Wil Hershberger

Macaulay Library	539715	5/26/18	Wil Hershberger
Macaulay Library	539840	3/31/2018	Wil Hershberger
Macaulay Library	20601731	10/27/15	Paul Marvin
Macaulay Library	20628011	9/26/15	Paul Marvin
Macaulay Library	22400231	12/27/15	Colin Sumrall
Macaulay Library	34379131	9/5/16	Colin Sumrall
Macaulay Library	40023621	11/15/16	Kiehl Smith
Macaulay Library	40365141	11/19/16	Robert O'Connell
Macaulay Library	42326791	12/11/16	Jeffrey Graham
Macaulay Library	43622601	12/17/16	Patrick J. Blake
Macaulay Library	45631001	1/16/17	Colin Sumrall
Macaulay Library	48151561	2/12/17	Colin Sumrall
Macaulay Library	48151961	2/12/17	Colin Sumrall
Macaulay Library	48664211	2/18/17	Ted Floyd
Macaulay Library	49018431	2/18/17	Alexis Adair
Macaulay Library	67926261	9/4/17	Brian Wulker
Macaulay Library	68476971	9/10/17	Tucker Beamer
Macaulay Library	68741741	9/12/17	David Simpson
Macaulay Library	69293331	9/17/17	Loyan Beausoleil
Macaulay Library	70740701	10/3/17	Mike Stewart

Macaulay Library	71182981	10/7/17	Bryan Henson
Macaulay Library	71721071	10/13/17	LynnErla Beegle
Macaulay Library	71993921	10/14/17	Colin Sumrall
Macaulay Library	72009771	10/15/17	Shelia Hargis
Macaulay Library	72051181	10/15/17	Jon G.
Macaulay Library	72182531	9/15/17	Jay McGowan
Macaulay Library	72436321	10/19/17	Steven Biggers
Macaulay Library	73184661	10/26/17	David Simpson
Macaulay Library	74099191	11/4/17	Anne Armstrong
Macaulay Library	74731791	11/10/17	Anne Armstrong
Macaulay Library	76101211	11/24/17	Josh Fecteau
Macaulay Library	76596541	11/25/17	David Simpson
Macaulay Library	79992891	12/31/17	Gary Leavens
Macaulay Library	80508021	12/20/17	William Hull
Macaulay Library	80737811	1/4/18	Richard Bunn
Macaulay Library	80827551	12/21/17	Jay McGowan
Macaulay Library	81754871	1/12/18	Peter Hawrylyshyn
Macaulay Library	82724911	1/20/18	Brad Walker
Macaulay Library	82724911	1/20/18	Brad Walker
Macaulay Library	86112531	2/16/18	Kyle Jones

Macaulay Library	86943401	2/21/18	Jamie and Corri Inman
Macaulay Library	86966091	2/20/18	Ryan Sanderson
Macaulay Library	87646221	2/23/18	Matt Schloss
Macaulay Library	90491751	2/17/18	Liam Wolff
Macaulay Library	114533821	9/11/18	Thomas Anderson
Macaulay Library	114735841	9/2/18	Jim Ferrari
Macaulay Library	115042351	9/13/18	Anne Armstrong
Macaulay Library	115392001	2/18/18	Paul Marvin
Macaulay Library	115704891	9/21/18	Richard A Fischer Sr.
Macaulay Library	116277561	9/22/18	Tim Lenz
Macaulay Library	116298371	9/25/18	Mike Stewart
Macaulay Library	116755521	9/29/18	Sandra Keller
Macaulay Library	117008151	9/30/18	Ragupathy Kannan
Macaulay Library	117180771	9/30/18	Richard A Fischer Sr.
Macaulay Library	117378651	10/4/18	Ragupathy Kannan
Macaulay Library	118165431	9/14/18	Tom Kerr
Macaulay Library	118679321	10/13/18	Gary Leavens
Macaulay Library	119016131	10/13/18	Michael Mulqueen
Macaulay Library	119173611	10/15/18	Martin Wall
Macaulay Library	119754781	10/7/18	Michael S Taylor

Macaulay Library	120813831	10/27/18	Bill Tollefson
Macaulay Library	120911771	10/27/18	Michael S Taylor
Macaulay Library	121788681	11/2//18	Jeffrey Roth
Macaulay Library	122144801	11/5/18	Simon Burton
Macaulay Library	122466281	11/7/18	Martin Wall
Macaulay Library	122472181	11/7/18	Tom Nolan
Macaulay Library	122489971	11/4/18	John Hurd
Macaulay Library	123248851	11/11/18	David Sarkozy cc
Macaulay Library	124519201	11/18/18	Lionel Xavier Horn
Macaulay Library	125068331	11/8/18	Christine Stoughton Root
Macaulay Library	125221271	11/25/18	Thomas Koffel
Macaulay Library	125475461	11/25/18	Valerie Heemstra
Macaulay Library	126446931	12/2/18	John O'Brien
Macaulay Library	126498941	11/29/18	Kaleb Kroeker
Macaulay Library	129285141	12/16/18	Simon Burton
Macaulay Library	129638871	12/17/18	Simon Burton
Macaulay Library	133037651	12/31/18	William Hull
Macaulay Library	133064161	12/31/18	Kerry Loux
Macaulay Library	133079281	1/4/19	John Kirk
Macaulay Library	133169171	1/4/19	Robert Bochenek

Macaulay Library	133511921	1/6/19	Ethan Ellis
Macaulay Library	133611101	1/6/19	Robert Beauchamp
Macaulay Library	133611161	1/6/19	Robert Beauchamp
Macaulay Library	133680581	1/6/19	Georgia Doyle
Macaulay Library	133722851	1/6/19	Valerie Heemstra
Macaulay Library	133947911	1/8/19	Gary Stone
Macaulay Library	134182421	1/13/19	Kelly Krechmer
Macaulay Library	134613591	1/12/19	Colin Sumrall
Macaulay Library	134821421	1/13/19	Shane Carroll
Macaulay Library	135591441	1/17/19	John Kirk
Macaulay Library	135850001	1/18/19	Charlie Bruggemann
Macaulay Library	137846581	1/29/19	S. Queen
Macaulay Library	139021451	2/4/19	Anne Armstrong
Macaulay Library	139257931	1/26/19	Martin Wall
Macaulay Library	139508341	2/7/19	Anne Armstrong
Macaulay Library	140002321	2/10/19	Michael Cheves
Macaulay Library	140703221	2/14/19	Jeffrey Roth
Macaulay Library	140919511	2/16/19	Mary McKittrick
Macaulay Library	141179941	2/17/19	Brett Moyer
Macaulay Library	142035611	2/22/19	Derek Lecy

Macaulay Library	175291781	9/2/19	John Kirk
Macaulay Library	175848781	9/6/19	John Abrams
Macaulay Library	176439151	9/9/19	Norman Soskel
Macaulay Library	177396281	9/16/19	Nick Bayly (SELVA)
Macaulay Library	177714821	9/18/19	Anne Armstrong
Macaulay Library	177933741	9/16/19	Winston Caillouet
Macaulay Library	178076351	9/20/19	Charles Shields
Macaulay Library	178170681	9/21/19	Tom Nolan
Macaulay Library	178630751	9/23/19	Anne Armstrong
Macaulay Library	179284801	9/27/19	Joseph Salmieri
Macaulay Library	179337001	9/28/19	Valerie Heemstra
Macaulay Library	179528131	9/28/19	Tom Nolan
Macaulay Library	179590511	9/29/19	Elissa Weidaw
Macaulay Library	180197591	10/2/19	Jack and Shirley Foreman
Macaulay Library	180270891	10/3/19	Elissa Weidaw
Macaulay Library	180412431	10/4/19	Steven Biggers
Macaulay Library	181873511	10/13/19	Charlie Bruggemann
Macaulay Library	181937491	10/12/19	Colin Sumrall
Macaulay Library	182283741	10/15/19	Vidhya Sundar
Macaulay Library	182364331	10/14/19	Shilo McDonald

Macaulay Library	183044071	10/19/19	Vidhya Sundar
Macaulay Library	184100611	10/25/19	Vidhya Sundar
Macaulay Library	184214831	10/22/19	Tom Nolan
Macaulay Library	184303631	10/26/19	Colin Sumrall
Macaulay Library	184463621	10/26/19	Ed M. Brogie
Macaulay Library	184605951	10/23/19	Jon Aird
Macaulay Library	184747431	9/2/19	Laura Sebastianelli
Macaulay Library	185516741	11/2/19	Valerie Heemstra
Macaulay Library	186469911	11/16/19	Gary Chapin
Macaulay Library	188207141	11/16/19	Jake Friebohle
Macaulay Library	188219371	11/16/19	Will Anderson
Macaulay Library	188383801	11/17/19	Norman Soskel
Macaulay Library	189653941	11/24/19	Lisa Cancade Hackett
Macaulay Library	190470641	11/29/19	Norman Soskel
Macaulay Library	191700171	12/6/19	Eric Wolman
Macaulay Library	191712011	12/6/19	Valerie Heemstra
Macaulay Library	191932411	12/7/19	Colin Sumrall
Macaulay Library	193087211	12/13/19	Jake Friebohle
Macaulay Library	193582931	12/16/19	Valerie Heemstra
Macaulay Library	194652311	12/22/19	Isidro Montemayor

Macaulay Library	194944331	12/24/19	Unknown
Macaulay Library	194958371	12/24/19	Unknown
Macaulay Library	194975691	12/24/19	Dan Fox
Macaulay Library	195388101	12/15/19	Martin Wall
Macaulay Library	195834731	12/29/19	Will Anderson
Macaulay Library	196293701	12/29/19	Martin Wall
Macaulay Library	196396011	12/21/19	Matthew Spoor
Macaulay Library	196938531	1/3/20	Anne Mytych
Macaulay Library	196975621	10/18/19	Emmanuel Salas
Macaulay Library	197761951	1/6/20	Valerie Heemstra
Macaulay Library	198021491	1/7/20	Valerie Heemstra
Macaulay Library	198086551	1/8/20	John Garver
Macaulay Library	198392541	1/6/20	Jay Gilliam
Macaulay Library	199212981	1/13/20	Valerie Heemstra
Macaulay Library	199637011	1/9/20	Lisa Hoffman
Macaulay Library	200136841	1/17/20	Skipper Anding
Macaulay Library	200137011	1/17/20	Skipper Anding
Macaulay Library	200482571	12/9/19	Nathan Wahler
Macaulay Library	202548291	1/16/20	Natasza Fontaine
Macaulay Library	202725281	1/25/20	Amy Swarr

Macaulay Library	203543831	1/28/20	Marco Vachon
Macaulay Library	206345581	1/26/20	Roshan Vignarajah
Macaulay Library	206615021	1/31/20	Ted Staton
Macaulay Library	207906871	2/1/20	Valerie Heemstra
Macaulay Library	208074551	2/8/20	Tom Lally
Macaulay Library	208804141	2/12/20	Tyler Hodges
Macaulay Library	208842601	2/8/20	Miguel Angel Aguilar Gomez
Macaulay Library	209670211	2/16/20	Amy Swarr
Macaulay Library	209706081	2/8/20	Robert Beauchamp
Macaulay Library	209868831	2/8/20	Roshan Vignarajah
Macaulay Library	209923211	2/17/20	Jeffrey Mann
Macaulay Library	210556201	2/18/20	Lisa Saffell
Macaulay Library	210797951	2/17/20	David Simpson
Macaulay Library	210926291	2/22/20	Robert Irwin
Macaulay Library	211131861	2/19/20	Amy Swarr
Macaulay Library	211893411	2/26/20	Taylor Sturm
Macaulay Library	212050061	2/27/20	Mark Hawryluk
Macaulay Library	212167111	2/25/20	Don Brode
Macaulay Library	235550451	12/22/19	Nicholas Martens

Florida Museum of Natural History	FLMNH00005	1/25/74	J.W. Hardy
Florida Museum of Natural History	FLMNH00009	1/26/74	J.W. Hardy
Florida Museum of Natural History	FLMNH01028	1/27/75	Barbara and David Lee
Florida Museum of Natural History	FLMNH01036	1/27/75	Barbara and David Lee
Florida Museum of Natural History	FLMNH01123	11/24/74	David Lee
Florida Museum of Natural History	FLMNH01204	4/14/75	J.W. Hardy
Florida Museum of Natural History	FLMNH01204	4/14/75	J.W. Hardy
Florida Museum of Natural History	FLMNH01452	8/17/75	Richard A Bradley
Florida Museum of Natural History	FLMNH03823	5/10/78	Richard A Bradley
Florida Museum of Natural History	FLMNH04708	1/11/79	J.W. Hardy
Florida Museum of Natural History	FLMNH04738	4/20/79	J.W. Hardy
Florida Museum of Natural History	FLMNH04746	6/8/79	J.W. Hardy

Florida Museum of Natural History	FLMNH05140	9/2/77	Phillip Gaddis
Florida Museum of Natural History	FLMNH05210	4/18/80	J.W. Hardy
Florida Museum of Natural History	FLMNH05246	4/30/78	Phillip Gaddis
Florida Museum of Natural History	FLMNH06118	3/7/81	J.W. Hardy
Florida Museum of Natural History	FLMNH06132	3/12/82	J.W. Hardy
Florida Museum of Natural History	FLMNH06134	3/12/82	J.W. Hardy
Florida Museum of Natural History	FLMNH06135	3/13/82	J.W. Hardy
Florida Museum of Natural History	FLMNH07124	4/21/85	Lawrence Kilham & Walter Taylor
Florida Museum of Natural History	FLMNH07124	4/21/85	Lawrence Kilham & Walter Taylor
Florida Museum of Natural History	FLMNH07125	4/24/85	Walter Taylor
Florida Museum of Natural History	FLMNH07125	4/24/85	Walter Taylor
Florida Museum of Natural History	FLMNH07127	4/26/85	Walter Taylor

Florida Museum of Natural History	FLMNH07133	6/3/85	Walter Taylor
Florida Museum of Natural History	FLMNH07136	5/2/85	Walter Taylor
Florida Museum of Natural History	FLMNH07136	5/2/85	Walter Taylor
Florida Museum of Natural History	FLMNH07136	5/2/85	Walter Taylor
Florida Museum of Natural History	FLMNH07138	5/2/85	Walter Taylor
Florida Museum of Natural History	FLMNH07269	10/20/84	Michael McMillan
Florida Museum of Natural History	FLMNH07269	10/20/84	Michael McMillan
Florida Museum of Natural History	FLMNH11486	4/9/89	Laurie Eberhardt
Florida Museum of Natural History	FLMNH11487	2/5/89	Laurie Eberhardt
Florida Museum of Natural History	FLMNH23683	5/15/77	Phillip Gaddis
Florida Museum of Natural History	FLMNH23688	5/15/77	Phillip Gaddis
Florida Museum of Natural History	FLMNH23692	5/20/77	Phillip Gaddis

Florida Museum of Natural History	FLMNH23869	3/13/78	Phillip Gaddis
Florida Museum of Natural History	FLMNH23963	10/5/78	Phillip Gaddis
Florida Museum of Natural History	FLMNH24024	1/4/79	Phillip Gaddis
Florida Museum of Natural History	FLMNH28086	Unknown	Unknown
Florida Museum of Natural History	FLMNH30384	2/6/17	Unknown
Florida Museum of Natural History	FLMNH30391	3/17/18	Unknown
Florida Museum of Natural History	FLMNH30392	3/17/18	Unknown
Florida Museum of Natural History	FLMNH30396	3/17/18	Unknown
Florida Museum of Natural History	FLMNH30397	3/24/18	Unknown
Florida Museum of Natural History	FLMNH30398	3/24/18	Unknown
Florida Museum of Natural History	FLMNH30399	3/24/18	Unknown
Florida Museum of Natural History	FLMNH30401	3/26/18	Unknown

Florida Museum of Natural History	FLMNH30401	3/26/18	Unknown
Florida Museum of Natural History	FLMNH30433	4/21/18	Unknown
Florida Museum of Natural History	FLMNH30510	3/10/19	Unknown
Florida Museum of Natural History	FLMNH31170	12/31/19	Tom Webber
Florida Museum of Natural History	FLMNH31174	3/15/20	Tom Webber
Florida Museum of Natural History	FLMNH31179	3/19/20	Tom Webber
Florida Museum of Natural History	FLMNH31184	3/27/20	Tom Webber
Florida Museum of Natural History	FLMNH31188	3/28/20	Tom Webber
Florida Museum of Natural History	FLMNH31191	4/1/20	Tom Webber
Florida Museum of Natural History	FLMNH31207	5/2/20	Tom Webber
Florida Museum of Natural History	FLMNH31213	5/2/20	Tom Webber
Florida Museum of Natural History	FLMNH31215	5/11/20	Tom Webber
Xeno Canto	XC103957	6/17/12	Mike Nelson

Xeno Canto	XC109026	5/22/12	Andrew Spencer
Xeno Canto	XC112511	1/20/12	Liam Wolff
Xeno Canto	XC112512	5/3/12	Liam Wolffe
Xeno Canto	XC116317	8/25/10	Daniel Parker
Xeno Canto	XC1210	5/11/92	Don Jones
Xeno Canto	XC122452	8/5/12	Chris Harrison
Xeno Canto	XC123347	3/13/11	Chris Harrison
Xeno Canto	XC124068	1/29/12	Chris Harrison
Xeno Canto	XC124764	4/25/1999	Thomas G. Graves
Xeno Canto	XC12871	4/23/07	Chris Parrish
Xeno Canto	XC12996	4/26/07	Chris Parrish
Xeno Canto	XC130535	4/13/13	Mike Nelson
Xeno Canto	XC133669	5/4/13	Kate Lovette
Xeno Canto	XC136273	6/4/13	Dan Lane
Xeno Canto	XC140964	4/22/13	Bernard Bousquet
Xeno Canto	XC140967	4/22/13	Bernard Bousquet
Xeno Canto	XC141031	4/25/13	Bernard Bousquet
Xeno Canto	XC141460	6/27/13	Mike Nelson
Xeno Canto	XC141908	7/7/13	Amy Davis
Xeno Canto	XC143792	7/12/13	Paul Marvin
Xeno Canto	XC147168	9/9/13	Bobby Wilcox
Xeno Canto	XC147174	9/9/13	Bobby Wilcox
Xeno Canto	XC15245	9/26/07	Chris Parrish

Xeno Canto	XC161207	10/25/11	Daniel Parker
Xeno Canto	XC168616	7/27/10	Paul Driver
Xeno Canto	XC168619	2/28/13	Paul Driver
Xeno Canto	XC169157	3/2/14	Paul Marvin
Xeno Canto	XC169158	3/6/14	Paul Marvin
Xeno Canto	XC173577	3/10/14	Paul Marvin
Xeno Canto	XC174543	4/14/14	Daniel Parker
Xeno Canto	XC175156	4/19/14	Daniel Parker
Xeno Canto	XC175337	4/14/14	Jim Holmes
Xeno Canto	XC175465	4/21/14	Daniel Parker
Xeno Canto	XC178303	5/15/14	Russ Wigh
Xeno Canto	XC18247	3/6/08	Chris Parrish
Xeno Canto	XC200998	10/25/14	Jack Hurd
Xeno Canto	XC20434	5/5/08	Chris Parrish
Xeno Canto	XC208938	11/26/14	Sander Pieterse
Xeno Canto	XC210728	3/24/90	Robert Benson
Xeno Canto	XC217121	8/26/14	Terry Davis
Xeno Canto	XC231097	4/10/98	Peter Boesman
Xeno Canto	XC234667	4/7/15	Danny Zapata-Henao
Xeno Canto	XC236014	4/15/15	Danny Zapata-Henao
Xeno Canto	XC236569	4/18/15	Jim Holmes
Xeno Canto	XC236767	4/16/15	Ted Floyd
Xeno Canto	XC247310	4/4/15	J.R. Rigby

Xeno Canto	XC248139	6/6/15	Paul Driver
Xeno Canto	XC254936	4/10/15	Nick Komar
Xeno Canto	XC254937	4/10/15	Nick Komar
Xeno Canto	XC255711	7/8/15	Antonio Xeira
Xeno Canto	XC278596	9/8/15	Bobby Wilcox
Xeno Canto	XC286403	9/13/15	Bobby Wilcox
Xeno Canto	XC289890	3/28/06	Nathan Pieplow
Xeno Canto	XC290036	11/14/15	J.R. Rigby
Xeno Canto	XC297788	1/1/16	Matthew Schenck
Xeno Canto	XC301187	10/6/15	C. Michael Stinson
Xeno Canto	XC301326	1/25/2016	Jerald R
Xeno Canto	XC301664	1/28/16	C. Michael Stinson
Xeno Canto	XC305161	2/28/16	Matt Brady
Xeno Canto	XC309890	4/1/16	Hal Mitchell
Xeno Canto	XC309920	4/1/16	J.R. Rigby
Xeno Canto	XC309921	4/1/16	J.R. Rigby
Xeno Canto	XC314878	4/30/16	Jim Holmes
Xeno Canto	XC316922	5/16/16	Matt Wistrand
Xeno Canto	XC317252	5/18/16	Jerald R
Xeno Canto	XC31802	5/3/08	James Eckert
Xeno Canto	XC321338	6/10/16	Matt Baumann
Xeno Canto	XC321866	6/3/16	Bobby Wilcox
Xeno Canto	XC322019	6/4/16	Bobby Wilcox

Xeno Canto	XC322022	6/4/16	Bobby Wilcox
Xeno Canto	XC323733	5-31-15	Terry Davis
Xeno Canto	XC328707	5/14/15	Antonio Xeira
Xeno Canto	XC332580	8/13/16	Bobby Wilcox
Xeno Canto	XC332606	8/13/16	Bobby Wilcox
Xeno Canto	XC332653	8/24/16	Bobby Wilcox
Xeno Canto	XC332765	8/25/16	Jerald R
Xeno Canto	XC333688	8/7/16	Eric Burris
Xeno Canto	XC33595	4/25/09	Andrew Spencer
Xeno Canto	XC340492	10/7/16	Michael Lester
Xeno Canto	XC343414	11/19/16	Rob O'Connell
Xeno Canto	XC343415	11/19/16	Rob O'Connell
Xeno Canto	XC343416	11/19/16	Rob O'Connell
Xeno Canto	XC34803	5/18/09	Andrew Spencer
Xeno Canto	XC348109	12/27/16	Patrick Blake
Xeno Canto	XC353922	2/1/17	Brian Henderson
Xeno Canto	XC356473	2/22/17	Joseph Bourget
Xeno Canto	XC358185	1/19/17	Thomas Magarian
Xeno Canto	XC358190	1/19/17	Thomas Magarian
Xeno Canto	XC362046	8/7/16	Matt Wistrand
Xeno Canto	XC363524	4/8/17	Brian Murphy
Xeno Canto	XC363525	4/8/17	Brian Murphy
Xeno Canto	XC364592	4/14/17	Brian Murphy

Xeno Canto	XC365748	11/26/16	Vicki Dern
Xeno Canto	XC366387	2/4/15	Antonio Xeira
Xeno Canto	XC366604	3/15/15	Antonio Xeira
Xeno Canto	XC370505	5/12/17	Eric DeFonso
Xeno Canto	XC370940	5/13/17	Eric DeFonso
Xeno Canto	XC371070	5/15/17	Eric DeFonso
Xeno Canto	XC371639	5/23/17	William Whitehead
Xeno Canto	XC372261	5/27/17	Ken Blankenship
Xeno Canto	XC383962	5/5/15	Antonio Xeira
Xeno Canto	XC384029	7/10/15	Antonio Xeira
Xeno Canto	XC391460	10/23/17	Peter Boesman
Xeno Canto	XC404487	3/4/18	Amanda
Xeno Canto	XC406663	3/18/18	Matt Wistrand
Xeno Canto	XC408641	8/6/16	Linda L. Stehlik
Xeno Canto	XC412667	4/24/18	Nicholas Comparato
Xeno Canto	XC416559	5/3/18	Sue Riffe
Xeno Canto	XC416822	5/4/18	Sue Riffe
Xeno Canto	XC425814	7/1/18	Meena Haribal
Xeno Canto	XC429067	4/14/18	Bruce Lagerquist
Xeno Canto	XC432885	8/2/18	Nick Komar
Xeno Canto	XC451901	9/16/18	Paul Marvin
Xeno Canto	XC452778	12/14/17	Paul Marvin
Xeno Canto	XC454065	1/28/19	Edward Caillouet

Xeno Canto	XC457190	5/13/18	Will Sweet
Xeno Canto	XC464175	3/24/19	Bruce Lagerquist
Xeno Canto	XC466690	4/14/19	Brian Hendrix
Xeno Canto	XC468714	4/26/19	William Whitehead
Xeno Canto	XC469529	4/29/19	Brian Hendrix
Xeno Canto	XC472499	5/10/19	Brian Hendrix
Xeno Canto	XC477366	12/4/17	Matthew L. Brady
Xeno Canto	XC477368	12/4//17	Matthew L. Brady
Xeno Canto	XC477391	5/15/19	Sue Riffe
Xeno Canto	XC477595	5/15/19	Sue Riffe
Xeno Canto	XC481961	6/14/19	Daniel Parker
Xeno Canto	XC487506	5/2/19	Lance A. M. Benner
Xeno Canto	XC492589	8/14/19	Brian Hendrix
Xeno Canto	XC494030	8/24/19	William Whitehead
Xeno Canto	XC498647	4/1/17	Jacob Saucier
Xeno Canto	XC498648	4/1/17.	Jacob Saucier
Xeno Canto	XC498768	4/3/17	Jacob Saucier
Xeno Canto	XC498947	4/6/17.	Jacob Saucier
Xeno Canto	XC502630	10/15/19	William Whitehead
Xeno Canto	XC511443	10/7/19	Bobby Wilcox
Xeno Canto	XC516974	12/30/19	Bobby Wilcox
Xeno Canto	XC52363	5/21/10	Mike Nelson
Xeno Canto	XC534174	3/1/20	Bobby Wilcox

Xeno Canto	XC534668	3/15/20	Brian Hendrix
Xeno Canto	XC537553	10/21/19	Sue Riffe
Xeno Canto	XC539275	3/24/20	Aidan Place
Xeno Canto	XC540855	4/2/20	Meena Haribal
Xeno Canto	XC542146	4/5/20	Joseph Keating
Xeno Canto	XC543512	4/9/20	Jeremy Nance
Xeno Canto	XC556630	4/18/19	Cao Brito
Xeno Canto	XC556632	4/26/19.	Cao Brito
Xeno Canto	XC558225	5/14/20	Brian Hendrix
Xeno Canto	XC56154	5/20/10	Chuck Davis
Xeno Canto	XC56157	5/20/10	Chuck Davis
Xeno Canto	XC56228	5/31/10	Chuck Davis
Xeno Canto	XC563199	5/29/20	Brian Hendrix
Xeno Canto	XC563615	5/30/20	Brian Hendrix
Xeno Canto	XC563616	5/30/20	Brian Hendrix
Xeno Canto	XC56415	3/17/09	Hilke Breder
Xeno Canto	XC564895	6/3/20	Amanda
Xeno Canto	XC62773	9/29/10	Mike Nelson
Xeno Canto	XC65136	11/6/10	Todd Wilson
Xeno Canto	XC77133	4/22/11	Stuart Fisher

324

325

Supplementary Table 2S: Results of linear mixed model analysis for song measurements comparing breeding (N = 264) and nonbreeding (N = 177) populations when transitional months between seasons were removed (February and September). All means are presented $\pm$ 1 SEM. Bolded values identify $P < 0.05$.

Song Measurement	Breeding Mean	Nonbreeding Mean	X^2_I	<i>P-value</i>
Song Length (sec)	1.69$\pm$0.02	1.57$\pm$0.02	10.35128	<0.05
Maximum Frequency (Hz)	5464.60 $\pm$ 61.63	5475.05 $\pm$ 75.98	0.04127943	0.84
Minimum Frequency (Hz)	1812.73 $\pm$ 16.85	1801.41 $\pm$ 21.16	3.670049	0.06
Frequency Bandwidth (Hz)	3651.86 $\pm$ 62.64	3673.64 $\pm$ 78.19	0.4214665	0.52
Number of Inflection Points	96.95 $\pm$ 1.74	95.54 $\pm$ 2.29	0.1506212	0.7
Maximum Entropy	4.85 $\pm$ 0.02	4.91 $\pm$ 0.03	0.3621236	0.55
Number of Syllables/Song	4.75$\pm$0.09	4.28$\pm$0.09	8.285182	<0.05
Number of Notes/Syllable	4.90 $\pm$ 0.07	4.86 $\pm$ 0.08	0.007514044	0.93
Trill Rate (syllables/sec)	3.04 $\pm$ 0.06	3.16 $\pm$ 0.06	5.571908	0.81