



Original Article

Full life course analysis of birdsong reveals maturation and senescence of highly repeatable song characteristics

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Signalers may benefit in some contexts from advertising their ages, for example in courting potential mates. Receivers in turn may benefit from assessing a signaler's age, even in cases where their doing so is against the signaler's interests. Indicators of age contained in signals thus may have important fitness consequences for both signalers and receivers. In birds, males of many species have been shown to display delayed maturation of their songs, resulting in older males singing songs that are higher in quality in one or more characteristics. Conversely, it seems possible that songs might eventually deteriorate with age as an aspect behavioral senescence. Studies of birdsong long enough to test both possibilities are quite uncommon, with nearly all studies aspect of age-dependent changes in birdsong spanning 3 or fewer years of males' lives. Here, we present the longest longitudinal analysis of male birdsong to date, in which we analyze songs recorded for 4–11 years of the lives of captive male swamp sparrows. We find that males displayed delayed maturation of three song characteristics: song rate, song length, and consistency between songs. Delayed maturation was followed by behavioral senescence of three characteristics: song rate, stereotypy within songs, and consistency between songs. Because song quality declined in males beyond 2 years of age, this evidence is inconsistent with a signaling system in which females both prefer increasingly older males and are able to accurately determine male age through song assessment. Rather, our evidence suggests that swamp sparrows should be able to use song to distinguish intermediate-aged males from 1-year-old and very old males.

Key words: behavioral senescence, birdsong, delayed maturation, sexual selection, swamp sparrows.

INTRODUCTION

Theory and empirical evidence suggest that females may benefit from mating with older males for several reasons. First, a male's ability to survive to an older age may indicate that he is of higher quality as compared to those males that did not survive (Trivers 1972; Kokko 1997, 1998). Second, older males may be more experienced and therefore better able to obtain higher-quality territories or provide superior paternal care to potential offspring, characteristics that females may also prefer (Yasukawa 1981; Alatalo, Gustafsson, et al. 1986; Alatalo, Lundberg, et al. 1986). Yet, mating with the oldest available males may also impose costs on choosing females, as older males may be less fertile (Dean et al. 2010) and will have had more time to accumulate mutations in their germ line (Pizzari et al. 2008). Females may therefore be selected to choose middle-aged males, which offer a balance

between demonstrated viability and senescent disadvantages. The frequency with which females prefer ever older males as opposed to middle-aged males is not well understood, although evidence from sandflies suggests that females prefer intermediate-aged males in at least one species (Jones et al. 2000).

Whether females are able to accurately determine a male's age depends on whether assessment signals exist that reliably reflect male age. Two processes may interact to determine whether age assessment is possible: delayed maturation and behavioral senescence. First, if male signals continue to increase in quality after males have reached adulthood (delayed maturation), older males will reliably have higher-quality signals. Second, behavioral senescence occurs when males' ability to produce complex behaviors such as displays declines as males get older. Delayed maturation in sexual signals has been documented extensively in birds for both visual (Rohwer et al. 1980; Lyon and Montgomerie 1986) and auditory (Kipper and Kiefer 2010) signals. Behavioral senescence has been documented in species across several taxa including crickets

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(Verburg et al. 2011) and mice (Garratt et al. 2011), although evidence from birds is much more limited as compared to delayed maturation (but see Rivera-Gutierrez et al. 2012).

Birdsong is known to be an age-dependent trait in many species, but evidence is mixed as to whether delayed maturation continues beyond birds' second year of life and little is known about the process of behavioral senescence of birdsong. In many species (reviewed in Kipper and Kiefer 2010), song characteristics undergo delayed maturation in adult individuals, meaning that significant changes occur between the songs of 1-year-old and 2-year-old males. In some species, evidence suggests that birdsong remains constant after the second year (e.g., swamp sparrows [*Melospiza georgiana*, Ballentine 2009], white-crowned sparrow [*Zonotrichia leucophrys*, Nelson and Poesel 2009], banded wrens [*Thryophilus pleurostrictus*, Vehrencamp et al. 2013], willow warbler [*Phylloscopus trochilus*, Gil et al. 2001]). Other cross-sectional and short-term longitudinal studies suggest that some changes may occur in birdsong throughout adulthood as well. For example, studies in European starlings (*Sturnus vulgaris*, Mountjoy and Lemon 1995), great reed warblers (*Acrocephalus arundinaceus*, Forstmeier et al. 2006), red-winged blackbirds (*Agelaius phoeniceus*, Yasukawa et al. 1980), barn swallows (*Hirundo rustica*, Galeotti et al. 2001), superb fairy wrens (*Malurus cyaneus*, Dalziel and Cockburn 2008), and banded wrens (*Thryophilus pleurostrictus*, de Kort et al. 2009) suggest that changes in repertoire size, repertoire composition, or song length may continue to occur in 3-year-old males or beyond. In the absence of more complete life course data, however, it is impossible to know whether song characteristics vary continuously with age or whether behavioral senescence eventually reverses the direction of age-related change. For example, data recorded during an individual's first 3 years of life may suggest that delayed maturation continues from that individual's second to third year of life, but such data cannot tell us whether birds that are currently undergoing delayed maturation will eventually display behavioral senescence (see Figure 1).

To the best of our knowledge, no longitudinal study of birdsong has included data from the same birds throughout their entire adult lives. The most complete longitudinal study of birdsong to date covered 2–4 years of life from 45 great tit individuals that ranged in

age from 1 to 6 years (Rivera-Gutierrez et al. 2012). Wild great tits in this study displayed delayed maturation followed by a senescent decline in song consistency, and this study remains the only study to date to demonstrate behavioral senescence in birdsong. Yet, even in this impressive longitudinal dataset, the vast majority (43/45) individuals were recorded across only two or three seasons (Rivera-Gutierrez et al. 2012).

Here, we present the most complete life course study of birdsong to date, as we report results from 11 captive swamp sparrow males that were recorded yearly during adulthood until a mean age of 10 years (range 4–11). Swamp sparrows are highly unlikely to live as long or longer than 10 years in the wild, as the maximum age recorded for a free-living swamp sparrow is 7 years, 10 months old (United States Geological Survey [USGS] 2017). Our recordings therefore span the entire natural lifespan of swamp sparrows. We used data from the songs of these 11 birds to address three questions: 1) do the songs of male swamp sparrows display delayed maturation? 2) do these songs show evidence of behavioral senescence later in life? and 3) do the characteristics of song allow reliable estimation of a singer's age?

METHODS

Subjects

We collected 12 male swamp sparrows as nestlings from Conneaut Marsh, Crawford County, PA, USA, between June 13 and 17, 2004. These birds were originally part of an experiment testing the influence of early stress on song learning. They were hand-reared in the laboratory and assigned to control (feeding until satiated) and experimental (70% of the food offered to the control group) groups. Details are given in Searcy et al. (2010).

We recorded multiple years of song data from 11 of the 12 original male swamp sparrows (control $n = 7$, experimental $n = 4$). The 12th male died before it was recorded for a second year and so is not included here. These males were collected between the ages of 2 and 6 days post-hatch (3.5 ± 0.4 , $\bar{X} \pm \text{SE}$) and trained with recordings of song for 12 weeks, beginning at an average age of 13.5 ± 0.6 days of age. The training models were 14 song types

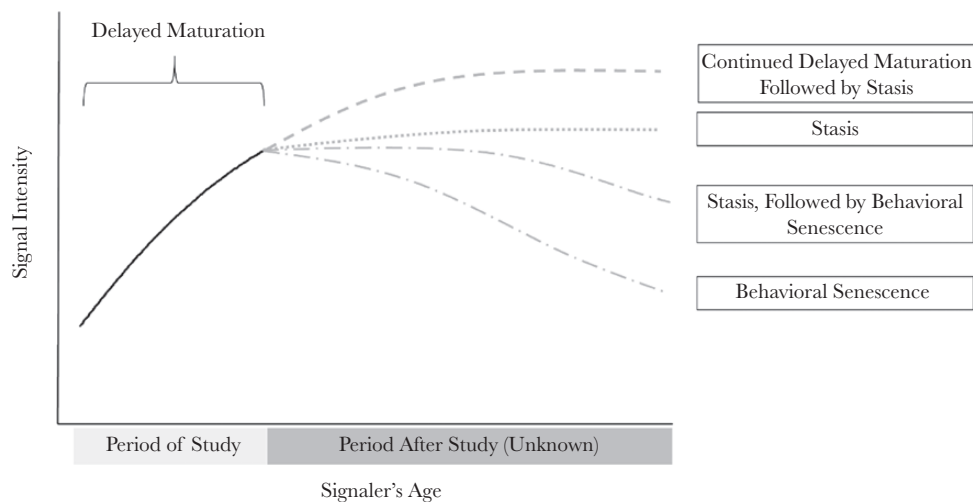


Figure 1

Possible unmeasured outcomes following an observation of delayed maturation. In the absence of full life course data on an animal's behavior, it is impossible to know whether behavioral senescence eventually occurs.

recorded from 14 different individuals in the study population. We presented song in bouts of the same type at a rate of one song per 10 s for 3 min, with 1 min of silence between each bout. The bouts were presented in a random order, which changed every week. Each song type bout was presented twice per day, once in the morning and once in the afternoon using a Marantz PMD 221 recorder and Acoustic Research “Powered Partner” Speaker (see Searcy et al. 2010 for details).

Hand-rearing and song tutoring took place in a large sound isolation room (Acoustic Systems, RE-142, $1.9 \times 1.8 \times 2.0$ m). At the end of song tutoring, we moved the birds into a large animal housing room. They remained housed in individual cages where they could see and hear each other for the duration of the experiment and were only removed from the group for song recording each spring, typically for a few days at a time.

Song recording

Not all subjects survived the full 11 years of our sampling. We recorded song from 6 of the 11 males for 11 successive years (2005–2015), from 2 males for 10 years (2005–2014), 1 male for 9 years (2005–2013), 1 for 7 years (2005–2011), and 1 for 4 years (2005–2008) (Supplementary Figure S1; Figure 4). Henceforth, the first year of analysis, when the birds were in their first year of crystallized song, is referred to as year 1 and subsequent years as years 2 through 11 (recording year is thus equivalent to age in years). All but one of the birds recorded for less than 11 years died from natural causes (one bird was humanely euthanized in his 10th year because of poor condition). Given the advanced age of the remaining birds, we stopped recording after the 11th year. We kept males on a normal seasonally varying photoperiod and recorded the song of each male starting each spring (maximum monthly range = April through August, minimum range = May) in an individual sound isolation chamber (Industrial Acoustics AC-1, $58 \times 41 \times 36$ cm, Shure SM57 microphone, Edirol USB Audio Capture UA-1000 (years 1 through 8) or M-audio Profire 2626 (years 9 through 11), Optiplex Dell Computer and Sound Analysis Pro software (versions 1.04 to SAP2011). We used the sound triggered recording function of Sound Analysis Pro to automatically record song (44.1 kHz) and captured a total of 243,749 song files for all birds for all years.

Song identification and selection

Swamp sparrow songs are typically sung as a single-phrased trill, with the repeated unit of the trill called a syllable; thus a syllable type is synonymous with a song type (Figure 2). Occasionally, a male will sing a two-parted song that begins with a trill of one syllable in its repertoire and ends with a trill of a second syllable also in its repertoire. Given that such two-parted songs are only rarely sung in this population and given that they only include syllables that are also produced by the same bird in one-parted trills, we do not consider these two-parted songs as an additional song type. Wild swamp sparrow males from this population typically include an average of three different song types (range 1–4) in their repertoire (Ballentine et al. 2004). Using the Syrinx software package (J.M. Burt), we viewed spectrograms (512 pt FFT, time axis 10 ms/line, frequency range 0–10 kHz) of every captured file in order to identify the song type of each recording. For the analyses described below, we primarily considered songs recorded in May (99.7% of songs, see exceptions below) because all males were sampled over at least 2 different days in May each year (average of 4.8 ± 0.3 days, range = 2–15 days), with an average of 28.6 ± 1.6 h of recording per bird per year (range = 11.4–90.0 h).

Song rate analysis

Typically, we set the automatic recording system to begin in the late afternoon of one day and continue through the morning of the following day, so that song was always captured throughout the evening and the following morning. Consistent with findings that swamp sparrows begin singing before dawn (Brooks 1930; Wetherbee 1968), we found significant singing occurring before the chamber lights went on at 0600 h. We chose a 6-h time frame between 0300 and 0900 h for calculating song rate because this captured a substantial proportion of songs sung by each male ($n = 127$ 537 songs; 1200 ± 174 songs per male per year, or $78 \pm 2\%$ of songs recorded in May per male for all years) and corresponds with the diurnal singing pattern reported in the wild (Mowbray 1997). To calculate the song rate per hour for each male for each year, we combined song counts from all days for which we had complete 6-h samples and divided by the total number of recording hours.

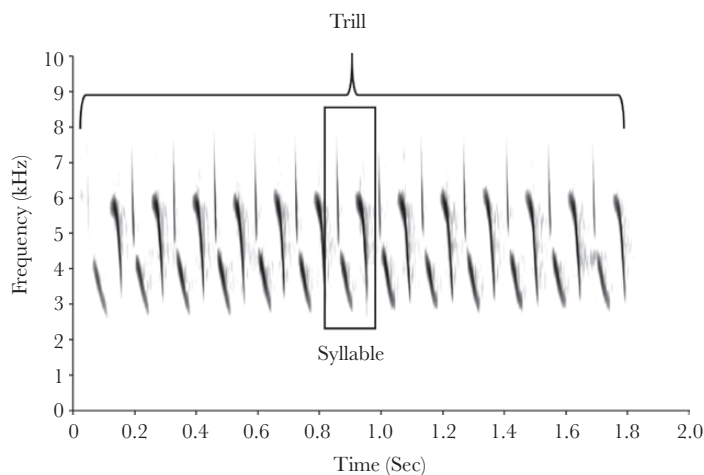


Figure 2

A spectrogram of a swamp sparrow song. Swamp sparrows typically sing a single-phrased trill. The repeated unit of this trill is called a syllable, which is equivalent to a song type.

Song length, vocal performance, copy quality, and stereotypy analysis

For song length, vocal performance, copy quality, within-song stereotypy, and between-song consistency analyses, we selected 10 exemplar songs for each song type (for one male in his 11th year, we were only able to find five exemplars of each of his two songs types; $n = 2300$ songs for all males for all years). Swamp sparrows typically repeat the same song type multiple times in a bout before switching to a different song type. We attempted to sample all exemplars of one song type from the same bout recorded in May, with a few exceptions when song types became less common (see below). About 99.7% of these song exemplars were selected from the May sample of songs (eight songs were recorded between June 1 and June 4). Nearly all selected songs were sung on the same day (91%) and a large majority were selected from the same bout. Nearly all selected songs were from bouts sung between 0600 and 0900 h (97%), and large majorities were from bouts sung between 0500 and 0700 h (84%).

Songs were analyzed using Signal for Windows v. 5 (Engineering Design, Berkeley, CA). Silence was added to each song file so that all files had a total length of 4 s. Trill rate and song length were measured on screen from the wave form display (cursor steps = 1.1 ms effective time resolution). Bandwidth (difference between high and low frequency) of each song was measured from the spectrogram display (FFT = 512 pts, DF = 86.1 Hz, DT = 11.6 ms, T inc. = 1.0 ms, cursor steps = 17.5 Hz). The dynamic range of the spectrogram display was adjusted so that all frequencies within 36 dB of the peak amplitude of the song were drawn at equal intensity and all frequencies at -36 dB relative to the peak amplitude were omitted. This allowed us to measure the bandwidth at -36 dB relative to the peak amplitude frequency of the song.

Vocal performance refers to the ability to sing songs that are physically or physiologically challenging to produce. In swamp sparrows, vocal performance reflects a trade-off between the repetition rate and frequency bandwidth of the trilled syllable comprising a song, and can be measured as the orthogonal distance (henceforth “deviation score”) from the upper-bound regression line based on the distribution of song plotted by these two parameters (Podos 1997). We used the upper-bound regression line previously calculated for this population ($y = -99.335x + 6554.7$; Ballentine et al. 2004).

We also used Signal to calculate spectrographic cross-correlations (Clark et al. 1987) to measure copy quality, between-song consistency, and within-song stereotypy. Song syllables from each of the 10 exemplars per type per bird were transformed to spectrograms (FFT = 256, DF = 172.3 Hz, DT = 5.8 ms, T inc = 1.0 s) and we performed pairwise cross-correlations between the syllables (analysis range = 0–10 kHz). To measure copy quality, we selected one syllable from the midpoint of each song exemplar and each training model and compared each of the student’s 10 syllable exemplars to the model syllable copied ($n = 10$ comparisons for each male’s song type per year, except for the one male from whom we only sampled five songs for each song type in his 11th year). To measure between-song consistency, we compared the same 10 student exemplar syllables to each other ($n = 45$ possible pairs for each male’s song type per year, except for the one male for whom we only had five songs per song type in his final year, thus $n = 10$ pairs). To measure within-song stereotypy, we averaged the cross-correlation comparisons of all consecutive syllable pairs within each of the 10 exemplar songs per bird (except for the one male for whom we only had five songs per song type in his final year, 11.6 ± 1.6 pairwise comparisons per song) and then took the mean of this average as the average measure of stereotypy for each bird for each year.

Statistical analysis

For analyses of changes in song characteristics over birds’ lives, we only considered changes in the highest performance song type that birds sang. Consistent with our longitudinal approach, we employed linear mixed-effects models to test for effects of maturation and senescence on song characteristics of this highest performance song type. For each song characteristic, we built two models that tested for changes in song characteristics over an animal’s lifetime: a maturation model that included data from only the first and second years of recordings (1- and 2-year-old birds) and a senescence model that included data from the second year onwards (birds age 2–11 years). We predicted that the transition from delayed maturation to behavioral senescence would occur at age 2 based on field data from swamp sparrows (Ballentine 2009), which found that male vocal performance improved as males aged from age 1 to 2 years and did not find evidence of continued improvement in older birds. Post hoc visual assessment of our data did not suggest that a different age cutoff would be more appropriate.

All models were built with the R package lme4 (Bates et al. 2014) and included a random effect of bird ID. Senescence models included a random slope of age if the inclusion of this random slope significantly improved the model (likelihood ratio test, $P < 0.10$). Residuals of all models were visually inspected for normality, and response variables were transformed to improve normality if substantial deviations were identified. Specifically, song rate was square root transformed and stereotypy within songs as well as consistency between songs were logit transformed. In all cases, model results using transformed and non-transformed data were qualitatively the same.

We estimated repeatability, R , as the proportional of total variance in the data that can be attributed to individual bird identity. We estimated repeatability using data from fully mature birds (years 2+). Repeatability estimates were obtained using the rptGaussian function from the rptR package (Stoffel et al. 2017), which uses a parametric bootstrapping method to estimate R .

RESULTS

Song repertoire stability over time

In their first year, the 11 swamp sparrows sang an average of 2.3 ± 0.24 song types/bird. Seven males sang only one or two song types in their first-year repertoire, and these males continued to sing these same song types throughout their lives, although the relative frequency of each type could change from year to year (Supplementary Figure S1). The three males that included three or four song types in their first-year repertoire exhibited more change in their repertoires over time, with each male effectively dropping one or more song types from their repertoire (two males dropped one song type, with the third male dropping two song types). Song types never completely disappeared, however (Figure 3). Even in years when we did not detect the song type on its own, it appeared in association with another song type, often as a single syllable or short trill at the end of the other type.

Age-related changes in song characteristics

Between the first and second year of recordings, we observed increases in song rate ($P = 0.03$), song rate ($P = 0.03$) and song length ($P = 0.06$, post hoc analysis $P = 0.04$, see Table 1), and consistency between songs ($P = 0.01$), indicating that swamp sparrows display

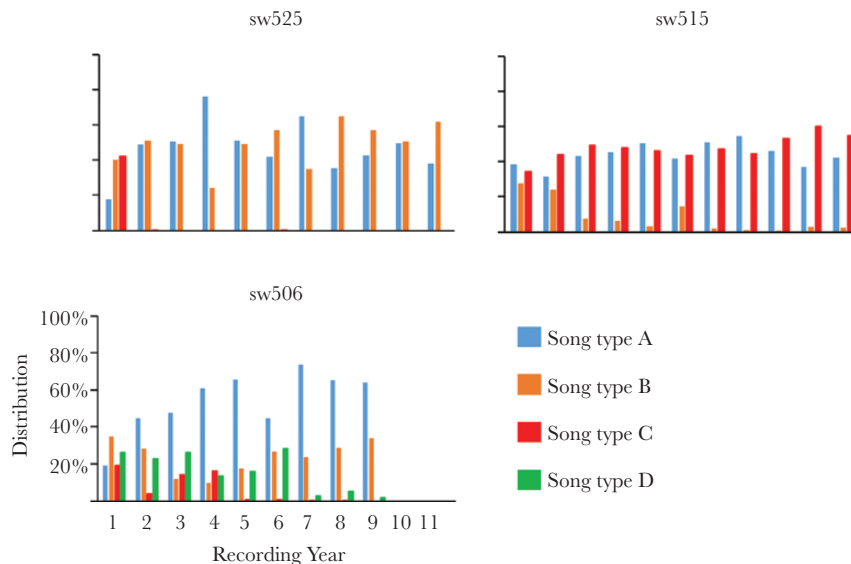


Figure 3 Repertoire changes in the three males who sang three or more song types as 1-year-olds. In contrast to males with smaller repertoires (Supplementary Figure S1), each of these three males dropped one or more song types as they aged.

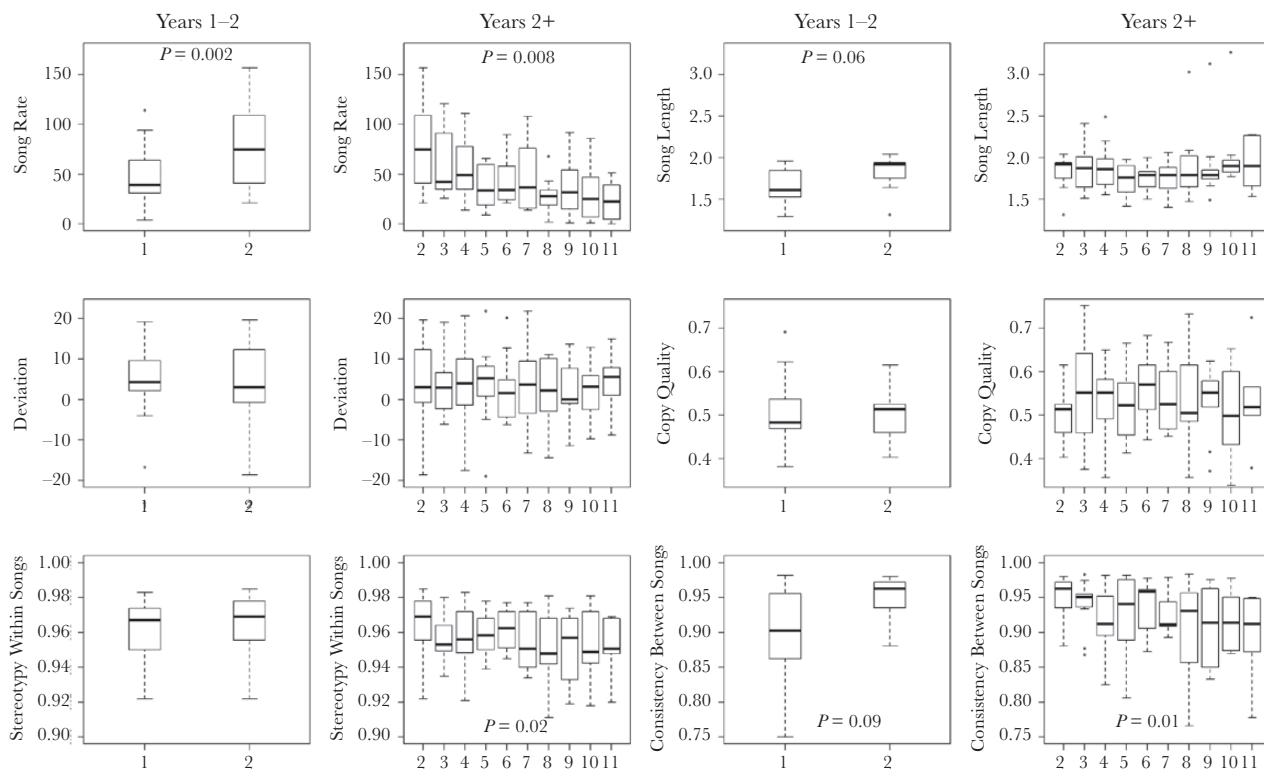


Figure 4 Several swamp sparrow song characteristics show increases in magnitude from years 1–2 and/or declines in magnitude after year 2.

delayed maturation of their songs. As birds aged beyond 2 years, we observed declines in song rate ($P = 0.008$), stereotypy within songs ($P = 0.02$), and consistency between songs ($P = 0.006$). We did not see comparable increases and/or declines in deviation score or copy quality. These results are displayed visually in Figure 4 and quantitatively in Table 1.

Song rate showed the clearest indication of age-related change, as birds displayed a marked increase in song rate from the first to second year in recording and then a consistent decline thereafter. Nearly half (5/11) of the birds displayed their highest measured song rate in the second year of recording and a majority (6/11) displayed their lowest measured song rate in their final 2 years of recording.

Table 1**Changes in song characteristics between the first and second year of recording and from the second year onwards**

Song characteristic	Year 1 (SE)	Year 2 (SE)	Slope estimate, years 2+ (SE)	Year 1–2, <i>P</i> value	Years 2+, <i>P</i> value
Song rate (square root)	6.59 (0.74)	8.69 (0.81)	−0.42 (0.13)	0.027	0.008[^]
Song length	1.65 (0.07)	1.83 (0.06)	0.018 (0.022)	0.060^a	0.43 [^]
Deviation score	4.76 (2.93)	4.44 (3.50)	0.11 (0.19)	0.82	0.57 [^]
Copy quality	0.51 (0.03)	0.50 (0.02)	−0.0009 (0.003)	0.68	0.72
Stereotypy within songs (logit)	3.29 (0.50)	3.40 (0.53)	−0.034 (0.012)	0.45	0.018[^]
Consistency between songs (logit)	2.47 (0.88)	3.10 (0.64)	−0.058 (0.023)	0.090 ^b	0.012^b

Transformations used to meet the assumption of residual normality are included in parentheses if applicable. Slopes and *P* values are extracted from linear mixed-effects models that include age as a fixed effect and bird ID as a random effect. Models that included age as a random slope are indicated with a [^] in the *P* value column indicating significant differences among individuals in the effect of age on the response variable. Inclusion or exclusion of random slopes did not qualitatively change any results. Bold values are significant at a value of 0.05 or an expanded post-hoc analysis returned a *P* value <0.05 (in the case of song length changes from year 1–2).

^aA post hoc model that considers data from all song types rather than just the highest performance song type returns a significant maturational effect (coefficient = 0.20, *t* = 2.66, *P* = 0.04).

^bModels of consistency between songs additionally included a binary indicator of whether all songs were taken from the same bout or if songs came from different bouts. Full model outputs of these two models can be found in [Supplementary Table S2](#).

Table 2**Repeatability estimates for each song characteristic**

Song characteristic	<i>R</i> estimate	95% Confidence interval	<i>P</i> value
Song rate	0.63	0.37, 0.79	<0.0001
Song length	0.61	0.30, 0.79	<0.0001
Deviation score	0.93	0.82, 0.97	<0.0001
Copy quality	0.47	0.17, 0.68	<0.0001
Stereotypy within songs	0.78	0.50, 0.89	<0.0001
Consistency between songs	0.33	0.09, 0.59	0.003

Repeatability of song characteristics across years

Each of the six song characteristics were significantly repeatable across years, although the strength of this repeatability varied considerably between characteristics. Deviation score showed the highest degree of repeatability across years (*R* = 0.93) and consistency between songs showed the lowest repeatability (*R* = 0.33). The estimates of all repeatability values and their confidence intervals are reported in [Table 2](#).

DISCUSSION

Using recordings of male swamp sparrows' songs from 4 to 11 years of their adult lives, we have demonstrated both delayed maturation and behavioral senescence in several song characteristics. We have especially strong evidence for behavioral senescence, as we observe declines in song rate (*P* < 0.01), stereotypy within songs (*P* = 0.02), and consistency between songs (*P* = 0.01) as birds get older. This evidence is especially noteworthy, as studies of behavioral senescence are far more rare than studies of delayed maturation ([Kipper and Kiefer 2010](#); [Rivera-Gutierrez et al. 2012](#)). We also find significant evidence of delayed maturation in two song measures, as we observe significant increases from year 1 to year 2 in song rate (*P* = 0.03) and song length (post hoc, *P* = 0.04).

Although we interpret our results as demonstrating delayed maturation and behavioral senescence in males's songs, it is impossible for us to fully distinguish between effects due to age and effects that result from males' spending longer periods of time in captivity. It is possible that males lose motivation to sing well as they spend more time in captivity because they fail to receive positive feedback from females for their efforts. If our results were explained entirely by

laboratory effects, however, we would expect to see declines in all of the song characteristics that we measured as males grew older, not just a subset of them. For example, deviation score measures the physiological difficulty of performing a song. If our observations could be explained by a decline in males' motivation, we would also expect males to sing less difficult songs, which they do not. Our confidence in our interpretation of behavioral senescence is further bolstered by the consistency between our results and the one publication of behavioral senescence in wild birds, which found that older great tit males sang at less consistently than did intermediate-aged males ([Rivera-Gutierrez et al. 2012](#)).

Some sexual selection models predict that signals involved in mate choice will only be evolutionarily stable if they reliably indicate information about the signaler's phenotype ([Grafen 1990](#); [Searcy and Nowicki 2005](#)). Because older males have demonstrated an increased ability to survive ([Trivers 1972](#); [Kokko 1997, 1998](#)) and because older males may possess experience that has indirect effects on female resource acquisition and offspring ([Yasukawa 1981](#); [Alatalo, Gustafsson, et al. 1986](#); [Alatalo, Lundberg, et al. 1986](#)), females are predicted to prefer older males as mates. However, evolutionary modeling has shown that if females have an especially strong preference for a sexual signal, it can be evolutionary stable for males to achieve a peak level of signal quality at an intermediate age, followed by behavioral senescence ([Kokko 1997](#)). Our results are consistent with this latter prediction. The songs of male swamp sparrows in our study became higher in quality by two measures as males matured from yearlings to after second year adults, indicating delayed maturation. Songs then become significantly lower in quality as fully mature males grow older, indicating behavioral senescence.

Our results suggest that if females swamp sparrows do prefer the oldest males, song does not provide a reliable signal by which to identify these males. Although our results indicate that mature males' songs change significantly as they grow older, these changes are in the direction of reduced, rather than increased, song quality. This reduction in song quality with age complicates identification of the oldest males. On a proximate level, a female swamp sparrow, if relying entirely on song rate, stereotypy, or consistency, would be unable to differentiate between the oldest males and yearling males. At an ultimate level, even if females used reductions in song rate, stereotypy, and/or consistency to judge males' ages, there are no physiological reasons to believe that younger males could not reduce the quality of these song characteristics in order to appear older if it were to their advantage, making the signal evolutionarily unstable. It therefore seems quite unlikely that female swamp sparrows both prefer increasingly older males and use song characteristics to accurately identify the oldest males among a group of mature males, despite being able to distinguish between yearlings and mature males generally.

If female swamp sparrows are unable to judge a male's quality by his age, they still may use song to judge other aspect of male quality. Previous studies suggest that deviation score may be the best measure of male quality, as males with lower deviations scores are larger and lower deviation songs are preferred by females (Ballentine et al. 2004; Ballentine 2009). Our results suggest that deviation score may also be the most *consistent* indicator of male quality in swamp sparrows, as it shows no senescent decline and very high measures of repeatability. Deviation score does vary across an individual's life, as the average individual displayed a range of annual measures of deviation score of 9.3 (SD = 3.5), but this variation from year to year was unrelated to males' ages and between-individual variation far exceeded within-individual variation, consistent with findings from field studies (DuBois et al. 2011; Liu et al. 2018).

Our results do suggest that male swamp sparrow songs could be a reliable indicator of intermediate age. Birds recorded during their third year (2-year-olds) had songs that were longer, and they sang more frequently than birds recorded during their second year (1-year-olds). Additionally, birds in their third year sang more frequently, more consistently, and more stereotypically than older birds. This pattern of delayed maturation and behavioral senescence demonstrates that variation in several song characteristics reliably predicts whether a male is in his third year. Thus, if female swamp sparrows actually prefer males of intermediate ages, as has been demonstrated in sandflies (Jones et al. 2000), male song characteristics may provide females with a reliable signal of middle-agedness.

We have found that male swamp sparrows display behavioral senescence in their songs, but we do not know whether females or males respond to this senescence in nature. If behavioral senescence of song is indicative of senescence in other traits of importance to attending females or males, such as capacity for paternal care or competitive ability, then we expect animals to respond to these changes. Wild swamp sparrows may be unlikely to live to 8–11 years of age in nature, but there is evidence of swamp sparrows living beyond 7 years of age in the wild (USGS 2017). Behavioral senescence in song characteristics is apparent before 7 years of age (Figure 4). Importantly, if we restrict our senescence analyses to years 2–7 of males lives, the slopes of our models are all at least as steep as those reported in Table 1 (see Supplementary Table S1), indicating that senescence does not appear to accelerate

in our oldest birds. We therefore conclude that, if animals attend to the song characteristics that display behavioral senescence (song rate, stereotypy within songs, consistency between songs), then we do expect that they will respond to behavioral senescence in the wild.

Whether either females or males behaviorally attend to senescence of these song characteristics of song and whether they differentiate between the songs of younger and older males is an open question and a target of future research. Playback experiments using birdsong from younger and older males, either to territorial males or to sexually receptive females, would allow researchers to determine whether within-individual age-related changes in song have any functional implications. Similar experiments have shown that males attend to delayed maturation of song (e.g., de Kort et al. 2009), but comparable work has not yet tested for attendance to behavioral senescence.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Zipple et al. (2019).

Handling editor: Marc Naguib

REFERENCES

- Alatalo RV, Gustafsson L, Lundberg A. 1986. Do females prefer older males in polygynous bird species? *Am Nat.* 127(2):241–245.
- Alatalo RV, Lundberg A, Glynn C. 1986. Female pied flycatchers choose territory quality and not male characteristics. *Nature.* 323(6084):152–153.
- Brooks MG. 1930. Notes on the Birds of Cranberry Glades, Pocahontas County, West Virginia. *Wilson Bull.* 245–252.
- Ballentine B. 2009. The ability to perform physically challenging songs predicts age and size in male swamp sparrows, *Melospiza georgiana*. *Anim Behav.* 77(4):973–978.
- Ballentine B, Hyman J, Nowicki S. 2004. Vocal performance influences female response to male bird song: an experimental test. *Behav Ecol.* 15(1):163–168.
- Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version, 1(7):1–23.
- Clark CW, Marler P, Beeman K. 1987. Quantitative analysis of animal vocal phonology: an application to swamp sparrow song. *Ethology.* 76(2):101–115.
- Dalziel AH, Cockburn A. 2008. Dawn song in superb fairy-wrens: a bird that seeks extrapair copulations during the dawn chorus. *Anim Behav.* 75(2):489–500.
- de Kort SR, Eldermire ERB, Valderrama S, Botero CA, Vehrencamp SL. 2009. Trill consistency is an age-related assessment signal in banded wrens. *Proc Roy Soc B: Biol Sci.* 276(1665):2315–2321.
- Dean R, Cornwallis CK, Løvlie H, Worley K, Richardson DS, Pizzari T. 2010. Male reproductive senescence causes potential for sexual conflict over mating. *Curr Biol.* 20:1192–1196.
- DuBois AL, Nowicki S, Searcy WA. 2011. Discrimination of vocal performance by male swamp sparrows. *Behav Ecol Sociobiol.* 65(4):717–726.
- Forstmeier W, Hasselquist D, Bensch S, Leisler B. 2006. Does song reflect age and viability? A comparison between two populations of

- the great reed warbler *Acrocephalus arundinaceus*. *Behav Ecol Sociobiol.* 59(5):634–643.
- Grafen A. 1990. Biological signals as handicaps. *J Theor Biol.* 144(4): 517–546.
- Galeotti P, Saino N, Perani E, Sacchi R, Møller AR. 2001. Age-related song variation in male barn swallows. *Ital J Zool.* 68(4):305–310.
- Garratt M, Stockley P, Armstrong SD, Beynon RJ, Hurst JL. 2011. The scent of senescence: sexual signalling and female preference in house mice. *J Evol Biol.* 24:2398–2409.
- Gil D, Cobb JLS, Slater PJB. 2001. Song characteristics are age dependent in the willow warbler, *Phylloscopus trochilus*. *Anim Behav.* 62:689–694.
- Jones TM, Balmford A, Quinnell RJ. 2000. Adaptive female choice for middle-aged mates in a lekking sandfly. *Proc Roy Soc B: Biol Sci.* 267(1444):681–686.
- Kipper S, Kiefer S. 2010. Age-related changes in birds' singing styles: on fresh tunes and fading voices? *Adv Study Behav.* 41:77–118.
- Kokko H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behav Ecol Sociobiol.* 41(2):99–107.
- Kokko H. 1998. Good genes, old age and life-history trade-offs. *Evol Ecol.* 12(6):739–750.
- Liu IA, Soha JA, Nowicki S. 2018. Song type matching and vocal performance in territorial signalling by male swamp sparrows. *Anim Behav.* 139:117–125.
- Lyon BE, Montgomerie RD. 1986. Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? *Evolution.* 40:605–615.
- Mowbray TB, 1997. Swamp sparrow. In: Poole A, Gill F, editors. *The birds of North America*. Philadelphia: The Academy of Natural Sciences, The American Ornithologist's Union. p. 1–24.
- Mountjoy JD, Lemon RE. 1995. Extended song learning in wild European starlings. *Anim Behav.* 49(2):357–366.
- Nelson DA, Poesel A. 2009. Does learning produce song conformity or novelty in white-crowned sparrows, *Zonotrichia leucophrys*? *Anim Behav.* 78(2):433–440.
- Podos J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (*Passeriformes: Emberizidae*). *Evolution.* 51(2):537–551.
- Pizzari T, Dean R, Pacey A, Moore H, Bonsall MB. 2008. The evolutionary ecology of pre- and post-meiotic sperm senescence. *Trends Ecol Evol.* 23:131–140.
- Rivera-Gutierrez HF, Pinxten R, Eens M. 2012. Tuning and fading voices in songbirds: age-dependent changes in two acoustic traits across the life span. *Anim Behav.* 83(5):1279–1283.
- Rohwer S, Fretwell SD, Niles DM. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Am Nat.* 115(3):400–437.
- Searcy WA, Nowicki S. 2005. *The evolution of animal communication: reliability and deception in signaling systems*. Princeton University Press.
- Searcy WA, Peters S, Kipper S, Nowicki S. 2010. Female response to song reflects male developmental history in swamp sparrows. *Behav Ecol Sociobiol.* 64(8):1343–1349.
- Stoffel MA, Nakagawa S, Schielzeth H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol Evol.* 8(11):1639–1644.
- Trivers RL. 1972. Parental investment and sexual selection. In: Cambell B, editor. *Sexual selection and the descent of man 1871–1971*. Chicago (IL): Aldine. p. 139–179.
- United States Geological Survey (USGS). 2017. Longevity records of North American birds. https://www.pwrc.usgs.gov/BBL/longevity/Longevity_main.cfm.
- Vehrencamp SL, Yantachka J, Hall ML, de Kort SR. 2013. Trill performance components vary with age, season, and motivation in the banded wren. *Behav Ecol Sociobiol.* 67:409–419.
- Verburgt L, Ferreira M, Ferguson JWH. 2011. Male field cricket song reflects age, allowing females to prefer young males. *Anim Behav.* 81(1):19–29.
- Wetherbee DK. 1968. *The southern swamp sparrow. Life histories of North American grosbeaks, cardinals, towhees, finches, sparrows, and allies*. US Natl. Mus. Bull, 237:1475–1490.
- Yasukawa K. 1981. Male quality and female choice of mate in the red-winged blackbird (*Agelaius phoeniceus*). *Ecology.* 62(4):922–929.
- Yasukawa K, Blank JL, Patterson CB. 1980. Song repertoires and sexual selection in the red-winged Blackbird. *Behav Ecol Sociobiol.* 7(3):233–238.
- Zipple MN, Nowicki S, Searcy WA, Peters S. Data from: Full life course analysis of bird song reveals maturation and senescence of highly repeatable song characteristics. Dryad Digital Repository. <https://doi.org/10.5061/dryad.g5t535g>.