Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2020), XX(XX), 1–7. doi:10.1093/beheco/arz218

Downloaded from https://academic.oup.com/beheco/advance-article-abstract/doi/10.1093/beheco/arz218/5697305 by Duke University user on 24 January 2020

Original Article

Sounds of senescence: male swamp sparrows respond less aggressively to the songs of older individuals

Matthew N. Zipple,[a] Susan Peters,[a] William A. Searcy,[b] and Stephen Nowicki[a]

[a]Department of Biology, Duke University, Room 137, Biological Sciences Building, 130 Science Drive, Durham, NC 27708, and [b]Department of Biology, University of Miami, 215 Cox Science Center, 1301 Memorial Drive, Coral Gables, FL 33146, USA

Received 4 November 2019; revised 16 December 2019; editorial decision 18 December 2019; accepted 20 December 2019.

Age-related changes in assessment signals occur in a diverse array of animals, including humans. Age-related decline in vocal quality in humans is known to affect perceived attractiveness by potential mates and voters, but whether such changes have functional implications for nonhuman animals is poorly understood. Most studies of age-related change in animal signals focus on increases in signal quality that occur soon after the age of first breeding ("delayed maturation"), but a few have shown that signal quality declines in older individuals after a mid-life peak ("behavioral senescence"). Whether other individuals are able to detect this senescent decline of assessment signals has not previously been tested. Here we use playback experiments to show that wild male swamp sparrows (*Melospiza georgiana*) respond more aggressively to songs from 2-year-old males as compared with songs from the same males when they are 10 years old. Senescence in signals that, like birdsong, affect reproductive success through intrasexual competition or mate choice may be of evolutionary significance.

Key words: **behavioral senescence, birdsong, signaling, territoriality, vocal discrimination.**

INTRODUCTION

As humans age, acoustic characteristics of their voice change in predictable ways (Ryan and Burk 1974; Hartman 1979; Hollien 1987; Baken 2005; Harnsberger et al. 2008; Stathopoulos et al. 2011), such that listeners are able to identify the age of a speaker with a high level of accuracy (Ptacek and Sander 1966; Shipp and Hollien 1969; Hollien 1987; Huntley et al. 1987; Cerrato et al. 2000; Harnsberger et al. 2008). One vocal characteristic that aids in the identification of a speaker's age is fundamental frequency, as voices are deepest during people's 40s and 50s (Titze 1994; Baken 2005; Stathopoulos et al. 2011). Perception of a person's age has important implications for both men and women, as age and age-related vocal changes influence a person's perceived attractiveness to a range of audiences, including potential mates (Rajecki et al. 1991; Baize and Schroeder 1995; Feinberg et al. 2005) and potential voters (Tigue et al. 2012; Klofstad et al. 2015). For example, voters consistently express a preference for middle-aged candidates both in surveys (Pew Research Center 2019) and in elections (Manning 2019), and voters are more likely to support a candidate with a deeper voice, consistent with their age preference (Tigue et al. 2012; Klofstad et al. 2015). Although these effects are well established for humans, it is not known whether age-related declines in vocal quality have functional implications for nonhuman animals.

Advertisement signals in animals have been the focus of study for decades (Searcy and Nowicki 2005). Much of this work has been done by studying male birdsong, a commonly used advertisement signal that sometimes changes with age (reviewed in the work of Kipper and Kiefer 2010). The large majority of studies of age-related changes in birdsong have focused on the first 2 or 3 years after adulthood is reached and in many cases have documented apparent improvements in song over this time period (Kipper and Kiefer 2010). Such "delayed song maturation" has been documented across different vocal characteristics in numerous song species. For example, red-winged blackbirds, *Agelaius phoeniceus*, great reed warblers, *Acrocephalus arundinaceus*, and European starlings, *Sturnus vulgaris*, display an increase in repertoire size as birds increase in age during early adulthood (Yasukawa et al. 1980; Mountjoy and Lemon 1995; Forstmeier et al. 2006). Similarly, alpine accentors, *Prunella collaris*, display increased song complexity as they age (Langmore et al. 1996), whereas banded wrens, *Thryophilus pleurostictus*, display decreased deviation scores and increased note consistency (Vehrencamp et al. 2013). In contrast to the wealth

Address correspondence to Steven Nowicki. E-mail: snowicki@duke.edu.

© The Author(s) 2020. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology.
All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

of research on age-related improvements in song attributes during early adulthood, studies of later age-related *declines* in song attributes remain uncommon, likely due to the difficulty of repeatedly recording the same birds over large segments of their lives. Such "behavioral senescence" of vocal attributes has been documented in two studies, one of the wild great tits, *Parus major* (Rivera-Gutierrez et al. 2012) and the other of captive swamp sparrows (Zipple et al 2019).

Studies of birds (Wetton et al. 1995; Mountjoy and Lemon 1996; Sundberg and Dixon 1996; Wagner et al. 1996; Richardson and Burke 1999; O'Loghlen and Rothstein 2003), lizards (Lopez et al. 2003), insects (Somashekar and Krishna 2011), mammals (Poole 1989; Ferkin 1999; Komers et al. 1999), and fish (Côté and Hunte 1993) have shown a female preference for older males, as evidenced by higher reproductive success of older males (reviewed in the work of Brooks and Kemp 2001), and this relatively high reproductive success has occasionally been associated with relatively more intense advertisement signals (Mountjoy and Lemon 1996; Sundberg and Dixon 1996; O'Loghlen and Rothstein 2003). Some studies have also demonstrated the ability of females to use assessment signals to distinguish between adult and subadult individuals (Lopez et al. 2003; O'Loghlen and Rothstein 2003), and a cross-sectional study of captive voles has shown that females prefer the scents of older individuals (Ferkin 1999). To our knowledge, however, no study has shown an ability of males or females to discriminate assessment signals based on within-individual age-related decline in the quality of those signals. To demonstrate that animals attend to such within-individual declines, it is necessary to show that receivers respond differently to a signal from an older individual as compared with a signal *from the same individual* when it was younger.

We have shown previously that swamp sparrow males (*Melospiza georgiana*) display senescent decline in several vocal characteristics as they age (Zipple et al. 2019). To test whether receivers respond to within-individual declines in song quality, we used playbacks of the songs of hand-reared male swamp sparrows of different ages to simulate intrusions on the territories of free-living male swamp sparrows. We compared the responses of territorial males to pairs of stimuli recorded from the same stimulus males, using in each case one set of songs recorded when the simulated intruder was 2 years old and another recorded when he was 10 years old.

METHODS

Song recordings

The methods used to record songs used to generate playback stimuli have been described elsewhere (Searcy et al. 2010; Zipple et al. 2019). Briefly, male swamp sparrows were collected as nestlings from Conneaut Marsh, Crawford County, PA in June 2004. They were hand-reared in the laboratory and were trained to sing over a 12-week period, beginning at approximately 2 weeks of age. Birds were trained using playback of 14 song types recorded from 14 different wild individuals in their home population.

After maturation, the songs of the hand-reared subjects were recorded in each year of adulthood, starting in their second year of life (age 1) and continuing until their death or their 12th year of life (age 11). In the spring of each year, birds were housed in individual sound isolation chambers (Industrial Acoustica AC-1 58 × 41 × 36 cm) and were recorded with Shure SM57 microphones and either an Eridol USB Audio Capture UA-1000 interface (years 1 through 8) or an M-Audio ProFire 2626 interface (years 9 through 11) attached to an Optiplex Dell computer running Sound Analysis Pro software (versions 1.04 to SAP 2011). We used the sound-triggered recording function of Sound Analysis Pro to automatically record a song (44.1 kHz). The acoustic environment and song recording process were therefore identical during all years of recording (Eridol and M-Audio have identical recording bandwidth and sampling rate), eliminating the potential for any year-specific artifacts.

Song stimuli

We generated playback stimuli from songs of these hand-reared males that were recorded when the birds were either 2 years old (recorded in May of the birds' 3rd year) or 10 years old (recorded in May of the birds' 11th year). We have shown that the songs of these birds declined in quality over the same age range, becoming less stereotypic within songs and less consistent between songs (Zipple et al. 2019).

We generated eight pairs of playback stimuli derived from eight different males, each of whom was recorded at age 2 and again at age 10. For each male at each age, we used 10 exemplars of one song type, the same 10 exemplars that we used for our senescence analysis (Zipple et al. 2019). These exemplars were all songs from the male's highest performance song type (i.e., the song type with the lowest deviation score), which was consistent across years for each male. Spectrograms of three pairs of 2-year-old and 10-year-old songs used as stimuli are shown in Figure 1, and Table S1 gives statistics on the characteristics of all eight pairs of songs. Males in this population sing a modest number of song types (usually three), all of which are quite distinctive, so that exemplars are readily assignable to song types. Assignments were made by a single individual via visual comparison of spectrograms. Each song was normalized to a peak amplitude of 2.0 V and high-pass filtered at 1500 Hz (Signal v.4, Engineering Design, Berkeley, CA). Hand-reared swamp sparrows occasionally include introductory or final notes in their adult song, and we removed these from three song types because such notes are not typical in wild song in this population.

In total, we generated 16 sets of playback songs (8 males, two sets of 10 song exemplars for each male). For 12 of these sets of playback songs, exemplars were selected from the same song bout. For three playbacks sets, songs were selected from different bouts sung on the same day, and one playback set was comprised of songs sung on four different days. To generate playback files, we presented a song once every 10 s in the same order in which the songs were originally sung. We then repeated this sequence two more times so that for each playback test the subject heard 30 songs (10 renditions of a song type, with this sequence of 10 songs repeated three times) over a 5-min period. Song rate, therefore, was held constant during playback experiments. Although we identified a senescent decline in song rate as birds age (Zipple et al. 2019), this decline was the result of singing fewer bouts of songs rather than of producing songs at a slower rate during individual bouts.

Playback experiments

We carried out playback experiments from May 25 to June 15, 2019, with wild swamp sparrows living in Crawford County, PA in the same site (Conneaut Marsh) from which the nestlings were initially collected. We played all of our stimuli from a Marantz PMD660 recorder via an Anchor Audio AN-MINI speaker. Songs were played at an average of 85 dB SPL (range 81–88) (BK Precision model 732A, A-weighting, fast response setting). Prior to conducting playback trials, we mapped territories by identifying

Downloaded from https://academic.oup.com/beheco/advance-article-abstract/doi/10.1093/beheco/arz218/5697305 by Duke University user on 24 January 2020

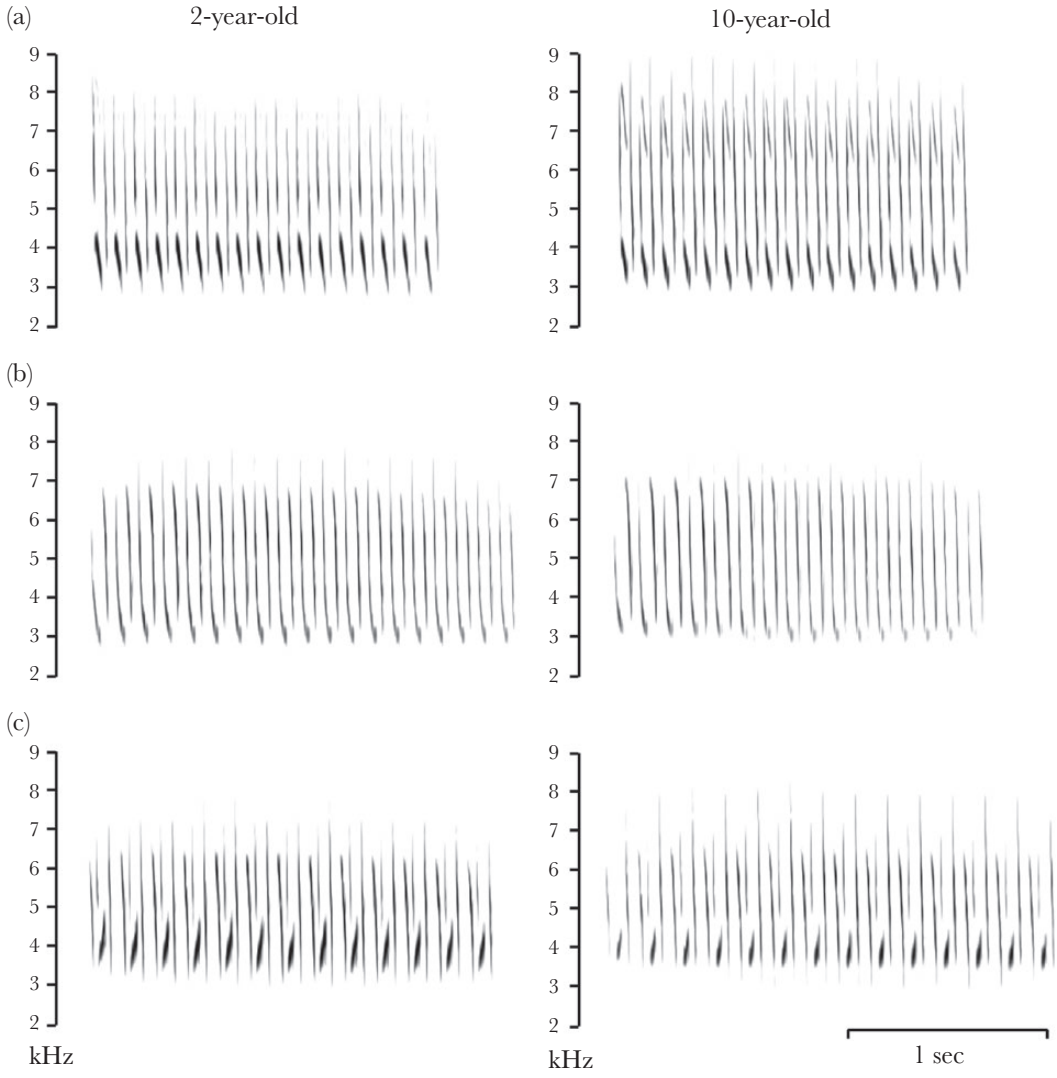

Figure 1
(a–c) Three examples of pairs of playback stimuli. Each pair represents (left) the highest performance song type recorded when the stimulus bird was 2 years old and (right) the same song type recorded when the stimulus bird was 10 years old.

areas over which males responded aggressively to playback of swamp sparrow songs.

We took three precautions to prevent any habituation of territorial males to playback. First, we mapped territories using probe songs from individuals that were not used as stimuli in playback experiments. Second, we used as few probe songs as possible when mapping males' territories (typically fewer than 20 songs per territory). Finally, after mapping a male's territory we waited for at least 1 day before testing his response to our stimuli. These precautions appear to have been effective, as we saw no evidence of habituation in our experiment (see Results section and Figure S2).

When setting up playback experiments, we placed the playback speaker within the subject's territory, choosing a location that would maximize visibility for the observers while also being as far from a territory boundary as possible to limit the response of any neighboring males. Some, although not all, of the subject males resided on territories adjacent to other subject males. Those males that were adjacent to other test subjects were banded after the conclusion of playbacks in order to confirm that they were each unique males. To aid in our estimation of males' distance to the speaker, we placed flagging on either side of the speaker at distances of 2, 4, 8, and 16 m.

During a playback trial, we played the stimulus for a 5-min period and then continued observation for a 5-min post-playback period. We used the subject's distance to the speaker averaged over the trial as our sole response measure. This measure has been shown to be a strong predictor of the likelihood of an attack in swamp sparrows (Ballentine et al. 2008) and closely related species (Searcy et al. 2006) and thus serves as a good proxy for an aggressive response. During trials, we recorded the bird's minimum distance to the speaker over 120 consecutive 5-s blocks (60 blocks from the playback period followed by 60 blocks from the post-playback period, 10 min total observation time). We recorded territorial males' distances as discrete estimates, based on the bird's position relative to our reference flagging (i.e., <2 m, 2–4 m, 4–8 m, 8–16 m, >16 m). Males who were known to be greater than 16 m from the speaker or who had not yet responded to the playback were identified as being more than 16 m from the speaker.

Downloaded from https://academic.oup.com/beheco/advance-article-abstract/doi/10.1093/beheco/arz218/5697305 by Duke University user on 24 January 2020

We measured each bird's response (n = 35 territorial males) to two different playback stimuli: one composed of recordings of a 2-year-old male and one composed of recordings of the same song types sung by the same male when he was 10 years old. All sets of trials were performed 2 or 3 days apart. The order in which birds were exposed to 2-year-old and 10-year-old songs was counterbalanced across stimuli. Observers were blind to the treatment (i.e., whether a 2-year-old or 10-year-old song was being played) during all data collection.

Statistical analysis

We first calculated a male's average distance to the speaker during each playback trial. To estimate a male's distance during a given block of time, we took the midpoint of the distance interval as the male's distance for that block (Peters et al. 1980). For example, if a male was 2–4 m from the speaker, we estimated his distance to be 3 m from the speaker during that 5-s block. We assumed that males that were more than 16 m from the speaker were 16–30 m from the speaker and thus on average at 24 m.

We built linear models to test for a difference in response to playback of the two sets of stimuli (all comparisons are within-subject). Specifically, we calculated the difference in average distance between the subject and the speaker during playback of the 2-year-old songs and the 10-year-old songs. We then built a linear model (equivalent to a two-tailed t-test) to test whether the birds showed a non-zero difference in their response to the two stimuli, on average. To test for effects of stimulus identity, we build a linear mixed-effects model using the R package lme4 (Bates et al. 2014; R Development Core Team 2018) that included a random effect of stimulus ID and used a chi-square test to determine whether the model that included the random effect explained the data better than the intercept-only linear model that did not include the random effect. We also used two-tailed t-tests to determine whether there were differences in response depending on the order of presentation of the stimuli or during the playback versus post-playback period.

RESULTS

Males positioned themselves closer to the speaker on average during playback of the songs of 2-year-old males as compared with the songs of the same males when they were 10-year olds (Figure 2; estimate of difference = 2.13 m, SE = 0.65 m, t = 3.28, P = 0.002). Differences in response to the two treatments did not differ between the playback and post-playback periods (Figure S1; t = 0.60, df = 34, P = 0.55) nor did we observe an effect of playback order (Figure S2; t = 1.14, df = 33, P = 0.26). We also did not observe any significant stimulus-specific effects on differences in males' responses (Figure S3; χ^2 = 0.03, P = 0.87). We therefore report the intercept-only model as our final model without random effects of stimulus ID. Results were qualitatively unchanged when including random effects of stimulus ID (Table S2).

DISCUSSION

We have shown that male swamp sparrows respond differently to acoustic assessment signals based on within-individual age-related declines in vocal quality. Specifically, males approached more closely to a speaker playing songs of 2-year-old males as compared with a speaker playing songs from the same males recorded as 10-year olds. Two previous studies have shown that some song characteristics deteriorate with age later in life in songbirds (Rivera-Gutierrez et al. 2012; Zipple et al. 2019), but to our knowledge this is the first demonstration outside of humans that such deterioration affects receiver response.

Closer proximity to a playback speaker is a reliable predictor of subsequent aggression in male swamp sparrows (Ballentine et al.

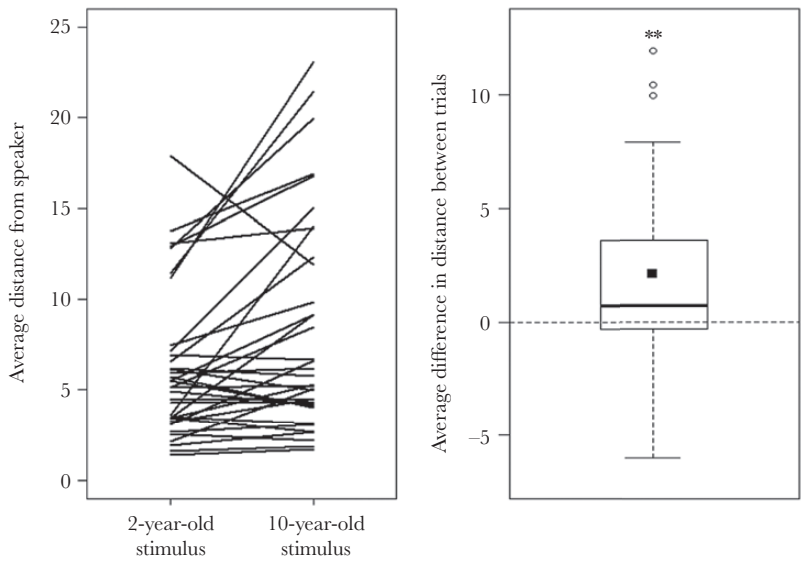

Figure 2

(a) The average distance between subjects and the speaker during playback of recordings of 2-year-old and 10-year-old birds. Positive slopes indicate that males positioned themselves more closely to the speaker when responding to the playback of songs from a 2-year-old male. (b) A visualization of the distribution of the slopes of the lines from (a), such that positive values indicate a stronger response to the 2-year-old stimulus as compared with the 10-year-old stimulus. Double asterisks indicate significance at the level of $P < 0.01$ (P = 0.002). The dark solid line represents the median difference in distance between trials and the dark square represents the mean.

Downloaded from https://academic.oup.com/beheco/advance-article-abstract/doi/10.1093/beheco/arz218/5697305 by Duke University user on 24 January 2020

2008), and we interpret our results as indicating that males respond more aggressively to 2-year-old songs as compared with 10-year-old songs. This response suggests that males perceive 2-year-old males as being a greater threat than 10-year-old males, which may indicate that older males are weaker competitors for access to females or other resources. Although there is some debate as to whether a more aggressive response by territorial birds indicates that the territorial male identifies the simulated intruder as more or less threatening (de Kort et al. 2009), our interpretation that increased aggression indicates an increase in perceived threat is supported by previous work in this population showing that males respond more aggressively toward higher quality songs (DuBois et al. 2011). Furthermore, the changes in song characteristics between years 2 and 10, such as declines in stereotypy within songs and in consistency between songs (Zipple et al 2019), are consistent with a decline in male quality, not an increase.

Female birds in several species have been shown to be at least as discriminating as males in response to song (Ratcliffe and Otter 1996), and in some cases clearly more so (e.g., Searcy and Brenowitz 1988; Searcy 1990; Searcy et al. 2002, but see the work of Nelson and Soha 2004). Given this pattern, our results with males give us some confidence that females are also able to detect within-individual declines in song quality and may also respond less strongly to songs of senescent males. This inference seemingly runs counter to the conclusion of many previous studies that female songbirds prefer older males as mates. Studies that reach this conclusion, however, most often compare female responses to males that have just reached adulthood (often 1-year olds) to female response to males that are for the most part only slightly older (e.g., 2- and 3-year olds) (Wetton et al. 1995; Wagner et al. 1996; O'Loghlen and Rothstein 2003). Thus, prior results on female preferences in songbirds can be reconciled with a pattern in which females prefer middle-aged males over both older and younger males. A preference for middle-aged males has been explicitly shown in sandflies, albeit on a much different time scale (Jones et al. 2000).

It was once thought that senescence did not occur in most natural populations because mortality was high enough that virtually no individuals lived long enough to experience age-related deterioration (Medawar 1952). Recent reviews have shown that, to the contrary, decreases in survival rates with age are widespread in wild populations, at least in birds and mammals (Brunet-Rossinni and Austad 2006; Nussey et al. 2013). Such "actuarial senescence" is often of a magnitude to appreciably reduce reproductive value in adulthood (Kowald and Kirkwood 2015) and thus be of evolutionary significance. Deterioration in behavioral abilities, especially in behaviors that contribute to mating success, can affect reproductive value independent of survival and thus add to the evolutionary importance of senescence. We have demonstrated one example of fitness-relevant behavioral senescence here, as have other studies (Arcese 1989; Nussey et al. 2009; Piper et al. 2017), but the phenomenon deserves further exploration.

Our study has two important caveats. First, in the recordings that we used, it is impossible for us to completely disentangle age-related decline in vocal quality from the effects of extended captivity in the laboratory. It is possible that declines in motivation after years of unsuccessful advertisement in the laboratory could result in lower quality singing in older individuals and in turn result in differential responses of territorial males to playback experiments. The fact that some measures of song quality improved from year 1 to year 2 in these captive birds (Zipple et al. 2019) does not fit with this declining-motivation hypothesis. In addition, our finding that birds decline in consistency between songs as they grow older (Zipple et al. 2019) is in agreement with the only observation of senescent decline of birdsong in wild birds (Rivera-Gutierrez et al. 2012), which suggests that the changes we observed in songs of older individuals do represent true behavioral senescence.

Second, in order to maximize males' ability to detect behavioral senescence, we used recordings of 10-year-old males to represent the senescent song. Although wild swamp sparrows have been recaptured that are known to be nearly 8-years old (USGS 2019), it is possible that 10 years exceeds the maximum age for this population. Yet, our previous work identified a smooth decline in vocal quality from ages 2 through 11, suggesting that behavioral senescence commences well before age 10, and that 10-year-old songs are unlikely to have experienced an unnatural acceleration of the process of senescence.

It is possible that, under natural conditions, few birds survive to old age and those that do may only be the birds in the best physical condition. Under such a scenario, these birds that do survive may be the least likely to display behavioral senescence because of their high quality. If this is the case, behavioral senescence would be less important for birds' ecology and evolution than the results of our experiment initially suggest. However, it is also possible that the birds that do survive to old age are those that invested the most in survival relative to reproduction (Stearns 1989). Under this scenario, the role of behavioral senescence under natural conditions would be more pronounced than suggested by our experiment. Therefore, before the evolutionary significance of senescence of birdsong can be understood, we need better data regarding the rate and distribution of senescent decline in natural populations.

The playback songs we used show some declines in known quality measures between the 2-year-old and 10-year-old sets (Table S1), but overall these differences seem rather minor. For example, although stereotypy does tend to decline as birds get older (Zipple et al. 2019), the 10-year-old songs used for playback were not less stereotypic than the 2-year-old songs, on average, and we do not see evidence that any differences in stereotypy between the song pairs explains a difference in subjects' response (see Table S1 and Figure S3). Nevertheless, our subjects strongly discriminated between 2-year-old and 10-year-old songs. This pattern suggests that additional aspects of song quality deteriorated between the ages of 2 and 10: ones that swamp sparrows are attuned to, but of which we are not yet aware. A search for such traits, in swamp sparrows and other organisms, may well be rewarding.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by funding from the National Science Foundation (IBN-0315377), Duke University, and an National Science Foundation Graduate Research Fellowship (M.N.Z.).

The authors gratefully acknowledge the Pymatuning Ecological Laboratory for logistical support, the Pennsylvania Game Commission for access to field sites, and S. Nakey for general advice.

Data accessibility: Analyses reported in this article can be reproduced using data provided by Zipple et al. (2020).

Handling editor: Marc Naguib

Downloaded from https://academic.oup.com/beheco/advance-article-abstract/doi/10.1093/beheco/arz218/5697305 by Duke University user on 24 January 2020

REFERENCES

Arcese P. 1989. Territory acquisition and loss in male song sparrows. Anim Behav. 37:45–55.

Baize HR, Schroeder JE. 1995. Personality and mate selection in personal ads: evolutionary preferences in a public mate selection process. J Soc Behav Personal. 10(3):517–536.

Baken RJ. 2005. The aged voice: a new hypothesis. J Voice. 19:317–325.

Ballentine B, Searcy WA, Nowicki S. 2008. Reliable aggressive signalling in swamp sparrows. Anim Behav. 75(2):693–703.

Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4.

Brooks R, Kemp DJ. 2001. Can older males deliver the good genes? Trends Ecol Evol. 16:308–313.

Brunet-Rossinni AK, Austad SN. 2006. Senescence in wild populations of mammals and birds. In: Masoro EJ, Austad SN, editors. Handbook of the biology of aging. Burlington (MA): Academic Press.

Cerrato L, Falcone M, Paoloni A. 2000. Subjective age estimation of telephonic voices. Speech Commun. 31(2–3):107–112.

Côté IM, Hunte W. 1993. Female redlip blennies prefer older males. Anim Behav. 46(1):203–205.

de Kort SR, Eldermire ER, Cramer ER, Vehrencamp SL. 2009. The deterrent effect of bird song in territory defense. Behav Ecol. 20(1):200–206.

DuBois AL, Nowicki S, Searcy WA. 2011. Discrimination of vocal performance by male swamp sparrows. Behav Ecol Sociobiol. 65(4):717–726.

Feinberg DR, Jones BC, Little AC, Burt DM, Perrett DI. 2005. Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. Anim Behav. 69(3):561–568.

Ferkin MH. 1999. Attractiveness of opposite-sex odor and responses to it vary with age and sex in meadow voles (*Microtus pennsylvanicus*). J Chem Ecol. 25(4):757–769.

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.

Harnsberger JD, Shrivastav R, Brown WS Jr, Rothman H, Hollien H. 2008. Speaking rate and fundamental frequency as speech cues to perceived age. J Voice. 22:58–69.

Hartman DE. 1979. The perceptual identity and characteristics of aging in normal male adult speakers. J Commun Disord. 12(1):53–61.

Hollien H. 1987. "Old voices": what do we really know about them? J Voice. 1(1):2–17.

Huntley R, Hollien H, Shipp T. 1987. Influences of listener characteristics on perceived age estimations. J Voice. 1(1):49–52

Jones TM, Balmford A, Quinnell RJ. 2000. Adaptive female choice for middle-aged mates in a lekking sandfly. Proc Biol Sci. 267:681–686.

Kipper S, Kiefer S. 2010. Age-related changes in birds' singing styles: on fresh tunes and fading voices? Adv Study Behav. 41:77–118.

Klofstad CA, Anderson RC, Nowicki S. 2015. Perceptions of competence, strength, and age influence voters to select leaders with lower-pitched voices. PLoS One. 10:e0133779.

Komers PE, Birgersson B, Ekvall K. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. Am Nat. 153:431–436.

Kowald A, Kirkwood TB. 2015. Evolutionary significance of ageing in the wild. Exp Gerontol. 71:89–94.

Langmore NE, Davies NB, Hatchwell BJ, Hartley IR. 1996. Female song attracts males in the alpine accentor *Prunella collaris*. Proc R Soc B Biol Sci. 263(1367):141–146.

Lopez P, Aragon P, Martin J. 2003. Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflect their mating preference for older males. Behav Ecol Sociobiol. 55(1):73–79.

Manning JE. 2019. Membership of the 116th Congress: a profile. Washington (DC): Congressional Research Service. https://crsreports.congress.gov.

Medawar PB. 1952. An unsolved problem of biology. London: Lewis.

Mountjoy JD, Lemon RE. 1995. Extended song learning in wild European starlings. Anim Behav. 49(2):357–366.

Mountjoy DJ, Lemon RE. 1996. Female choice for complex song in the European starling: a field experiment. Behav Ecol Sociobiol. 38(1):65–71.

Nelson D, Soha J. 2004. Male and female white-crowned sparrows respond differently to geographic variation in song. Behaviour. 141(1):53–69.

Nussey DH, Froy H, Lemaitre JF, Gaillard JM, Austad SN. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. Ageing Res Rev. 12:214–225.

Nussey DH, Kruuk LE, Morris A, Clements MN, Pemberton JM, Clutton-Brock TH. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. Am Nat. 174:342–357.

O'Loghlen AL, Rothstein SI. 2003. Female preference for the songs of older males and the maintenance of dialects in brown-headed cowbirds (*Molothrus ater*). Behav Ecol Sociobiol. 53(2):102–109.

Peters SS, Searcy WA, Marler P. 1980. Species song discrimination in choice experiments with territorial male swamp and song sparrows. Anim Behav. 28(2):393–404.

Pew Research Center. 2019. Nearly half of democrats say the best age for their President is "in their 50s." Available from: https://www.people-press.org/2019/05/23/nearly-half-of-democrats-say-the-best-age-for-a-president-is-in-their-50s/.

Piper WH, Brunk KM, Flory JA, Meyer MW. 2017. The long shadow of senescence: age impacts survival and territory defense in loons. J Avian Biol. 48(8):1062–1070.

Poole JH. 1989. Mate guarding, reproductive success and female choice in African elephants. Anim Behav. 37:842–849.

Ptacek PH, Sander EK. 1966. Age recognition from voice. J Speech Hear Res. 9:273–277.

R Development Core Team. 2018. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. https://www.R-project.org/.

Rajecki DW, Bledsoe SB, Rasmussen JL. 1991. Successful personal ads: gender differences and similarities in offers, stipulations, and outcomes. Basic Appl Soc Psych. 12(4):457–469.

Ratcliffe L, Otter K. 1996. Sex differences in song recognition. In: Kroodsma D, Miller E, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 339–355.

Richardson DS, Burke T. 1999. Extra-pair paternity in relation to male age in Bullock's orioles. Mol Ecol. 8:2115–2126.

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.

Ryan WJ, Burk KW. 1974. Perceptual and acoustic correlates of aging in the speech of males. J Commun Disord. 7:181–192.

Searcy WA. 1990. Species recognition of song by female red-winged blackbirds. Anim Behav. 40(6):1119–1127.

Searcy WA, Anderson RC, Nowicki S. 2006. Bird song as a signal of aggressive intent. Behav Ecol Sociobiol. 60(2):234–241.

Searcy WA, Brenowitz EA. 1988. Sexual differences in species recognition of avian song. Nature. 332(6160):152–154.

Searcy WA, Nowicki S. 2005. The evolution of animal communication: reliability and deception in signaling systems. Princeton (NJ): Princeton University Press.

Searcy WA, Nowicki S, Hughes M, Peters S. 2002. Geographic song discrimination in relation to dispersal distances in song sparrows. Am Nat. 159:221–230.

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.

Shipp T, Hollien H. 1969. Perception of the aging male voice. J Speech Hear Res. 12:703–710.

Somashekar K, Krishna MS. 2011. Evidence of female preference for older males in *Drosophila bipectinata*. Zool Stud. 50:1–15.

Stathopoulos ET, Huber JE, Sussman JE. 2011. Changes in acoustic characteristics of the voice across the life span: measures from individuals 4–93 years of age. J Speech Lang Hear Res. 54(4):1011–1021.

Stearns SC. 1989. Trade-offs in life-history evolution. Funct Ecol. 3(3):259.

Sundberg J, Dixon A. 1996. Old, colourful male yellowhammers, *Emberiza citrinella*, benefit from extra-pair copulations. Anim Behav. 52(1):113–122.

Tigue CC, Borak DJ, O'Connor JJM, Schandl C, Feinberg DR. 2012. Voice pitch influences voting behavior. Evol Hum Behav. 33(3):210–216.

Titze IR. 1994. Principles of voice production. Englewood Cliffs (NJ): Prentice Hall.

United States Geological Survey (USGS). 2019. Longevity records of North American birds. Available from: 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.

Wagner RH, Schug MD, Morton ES. 1996. Condition-dependent control of paternity by female purple martins: implications for coloniality. Behav Ecol Sociobiol. 38(6):379–389.

Downloaded from https://academic.oup.com/beheco/advance-article-abstract/doi/10.1093/beheco/arz218/5697305 by Duke University user on 24 January 2020

Wetton J, Burke T, Parkin D, Gairns E. 1995. Single-locus DNA fingerprinting reveals that male reproductive success increases with age through extra-pair paternity in the house sparrow (*Passer domesticus*). Proc R Soc London Ser B Biol Sci. 260(1357):91–98.

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 M, Nowicki S, Searcy W, Peters S. 2019. Full life course analysis of bird song reveals maturation and senescence of highly repeatable song characteristics. Behav Ecol. arz146.

Zipple MN, Peters S, Searcy WA, Nowicki S. 2020. Data from: sounds of senescence: male swamp sparrows respond less aggressively to the song of older individuals. Behav Ecol. doi:10.5061/dryad.gxd2547gq.

Downloaded from https://academic.oup.com/beheco/advance-article-abstract/doi/10.1093/beheco/arz218/5697305 by Duke University user on 24 January 2020