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Female swamp sparrows do not show evidence of discriminating between the songs of peak-aged and senescent males

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Abstract

Sexual selection theory predicts that females face contrasting selection pressures when choosing the age of their mate. On the one hand, older males have demonstrated their ability to survive and they may be more experienced than younger males. At the same time, however, younger males are expected to have accumulated fewer deleterious mutations in their germline as compared to older males. These contrasting pressures on female preference may result in a preference for intermediate-aged males. A preference for males of a particular age can only be expressed, however, if females are able to identify males of different ages. We have previously shown that male swamp sparrows display age-related changes in vocal quality, such that males display sharp increases in vocal quality in early adulthood, followed by gradual senescent declines thereafter. We have also shown that territorial males discriminate these within-individual differences, giving stronger aggressive responses to songs of peak-aged males than to those of senescent males. Here, we use a copulation solicitation assay to test whether females also discriminate these within-signaler markers of senescence in song. Contrary to our prediction, females did not show any evidence of discriminating between songs recorded from peak-aged males as compared to songs from the same males following song senescence. We suggest that this difference in demonstrated discrimination between males and females may be the result of the two sexes attending to different song characteristics.

KEYWORDS

behavioral senescence, birdsong, communication, mate choice, sexual selection, swamp sparrow

1 | INTRODUCTION

When it comes to deciding on the ideal age for a potential mate, sexual selection theory predicts that females can face contrasting selection pressures. On the one hand, older males have managed to survive for longer periods, which may indicate to females that they are of higher quality, on average, as compared to younger males that have not overcome equivalent mortality risk (Manning, 1985; Trivers, 1972). Similarly, the greater life experience of older males might make them better equipped to provide resources to mates, either in the form of higher quality territories or higher quality paternal care provided to resulting offspring (Kokko, 1997, 1998; Trivers, 1972). These benefits are expected to select for a female preference for older males. On the other hand, older males are also expected to have acquired a greater number of deleterious germline mutations and also may be less fertile, costs that might lead to selection for a female preference for younger males (Dean et al., 2010; Pizzari et al., 2008; Trivers, 1972). Evidence of actuarial and reproductive senescence is widespread among Passeriformes (including multiple studies of song sparrows, *Melospiza melodia*), suggesting that such mutations could pose a fitness cost to females (Nussey et al., 2013). The result of these contrasting selective pressures may be selection for females to prefer intermediate-aged individuals that have managed to survive for some portion of adulthood, but that do not yet bear the costs of senescent decline (Brooks & Kemp, 2001). While tests of this hypothesis are rare, a study of sandflies (*Lutzomyia longipalpis*) shows that females display an adaptive preference for intermediate-aged males, although the mechanism that allows females to exercise this choice is not clear (Jones et al., 2000). Similarly, a longitudinal study of male lance-tailed manakins (*Chiroxiphia lanceolata*) found that intermediate-aged males have the highest annual reproductive success, although the mechanism(s) that result in this pattern also are unknown (DuVal, 2012).

In order for females to express a preference for males of a given age, they must first be able to identify males' ages, through the use of a reliable signal (Searcy & Nowicki, 2005). Among songbirds, song is widely used as an advertisement signal, and males and females of many species display discrimination of song along some axis or axes of variation (Catchpole & Slater, 2008). What is more, song characteristics are related to age in many species (reviewed in Kipper & Kiefer, 2010). Song would therefore seem to be an ideal signal with which female songbirds could assess male ages and then exercise a preference for males of a particular age.

Despite the theoretical importance of a male signalers' age to receivers, however, and the age-related nature of many song characteristics, studies of the effect of male signalers' age on female responses are quite rare. Within songbirds, most studies that consider receiver responses to songs from males of different ages test whether territorial males discriminate between simulated intruders of different ages (Akçay et al., 2016; Cucco & Malacarne, 1999; de Kort et al., 2009; Zipple et al., 2020). To our knowledge, only a single study has tested for female discrimination of songs recorded from males of different ages. O'Loghlen and Rothstein (2003) showed that female brown-headed cowbirds prefer songs recorded from fully mature (3-year-old) males as compared to songs recorded from (different) yearling males. The state of the literature is similar outside of songbirds, as a study of lizards shows that females discriminate between adults and subadults (Lopez et al., 2003), and a cross-sectional study of voles has shown that females prefer the scents of older individuals (Ferkin, 1999). To date, no study has asked whether females detect and respond to within-individual age-related changes in song, nor has any study asked whether females respond to senescent declines in vocal quality. The absence of such studies is likely the result of the challenge of recording males' songs repeatedly throughout their lifetime, along with the relative difficulty of assessing female responses (generally tested in the laboratory) as compared to male responses (which can be more easily measured in the field).

We have shown previously that individual male swamp sparrows display an increase in their song quality from age 1 to age 2 ("delayed maturation"), before exhibiting a decline through the rest of their lives ("behavioral senescence," Zipple et al., 2019). We also have shown that territorial males detect this within-individual behavioral senescence: Males respond more aggressively to playback of songs recorded from an individual male when he was 2 years old as compared to songs recorded *from the same male* when he was 10 years old (Zipple et al., 2020). Because individuals display behavioral senescence that allows for discrimination of peak-aged and senescent males, the swamp sparrow system is ideal for examining whether females respond to senescent declines in signal quality. Because territorial males treated peak-aged males as a greater threat (Zipple et al., 2020), and because female songbirds are generally believed to be at least as discriminating as males (Searcy & Brenowitz, 1988; Searcy, 1990; Ratcliffe & Otter, 1996; Searcy et al., 2002, but see Nelson & Soha, 2004), we predicted that females would display a preference for songs recorded from peak-aged, 2-year-old males as compared to songs recorded from the same males after they had senesced.

2 | METHODS

2.1 | Pre-registration

To maximize the transparency of our analyses and the reproducibility of our results, we pre-registered the methods, hypotheses, and predictions for this study prior to collection of females (available at https://aspredicted.org/zt3vh.pdf).

2.2 | Song recordings

The methods used to record the songs for our playback stimuli are described in detail elsewhere (Searcy et al., 2010; Zipple et al., 2019). Male swamp sparrows were collected as nestlings from Conneaut Marsh, Crawford County, PA, USA, in June 2004 and were then hand-reared in the laboratory. For 12 weeks, starting at approximately 2 weeks of age, males were trained using playback of 14 song types recorded from 14 wild individuals.

Beginning in their second year of life (age 1), males were recorded annually through their twelfth year of life (age 11) or until they died (whichever happened first). In May of each year, males were housed in individual sound isolation chambers (Industrial Acoustics AC-1, 58 x 41 x 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 2,626 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 song (44.1 kHz sampling rate). 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.

2.3 | Song stimuli

We created playback stimuli from songs of the hand-reared males that were recorded when the birds were 2, 5, or 10 years old (recorded in May of the birds' third, sixth, or eleventh year, respectively). Songs from these birds initially increased in quality as birds matured between ages 1 and 2, and then declined in quality (as indicated by a decline in within-song stereotypy and between-song consistency) from age 2 through age 10 (Zipple et al., 2019). Thus, the vocal quality of the recorded songs was highest for the songs recorded from 2-year-olds, lowest for the songs recorded from 10-year-olds, and of intermediate quality for the songs from the 5-year-olds. Figure 1 shows examples of sonograms of songs sung by 2-year-old males and 10-year-old males.

To generate stimuli, we built audio files by compiling song exemplars recorded at a given age (the same exemplars used in Zipple et al., 2019, 2020). Each stimulus comprised 10 exemplars in the same order in which the songs were originally sung, played one after another, at a rate of one song per ten seconds. This set of 10 exemplars was played twice, resulting in a total playback time of 200 s. Songs were normalized to a peak amplitude of 2.0 volts and high-pass filtered at 1,500 Hz (Signal v.4, Engineering Design). Hand-reared swamp sparrows occasionally include introductory or final notes in their adult song; we removed these from three song types since such notes are not typical in wild song in this population. Songs were usually recorded from a single bout, although a minority of playbacks (6 out of 26) were produced by combining songs from across bouts.

For each comparison (2-year-olds versus 10-year-olds and 2-year-olds versus 5-year-olds, see "Playback Trials," below) we constructed as many pairs of stimuli as there were recorded males. For example, only 8 males survived to be recorded as 10-year-olds, so we were able to construct a total of 8 pairs of stimuli to compare females' responses to songs from 2-year-olds and 10-year-olds. A total of 10 males survived to be 5-year-olds, so we were able to build 10 pairs of stimuli for the 2-year-old versus 5-year-old comparison. Thus, 4 of our stimulus pairs were repeated across females for the 2-year-old versus 10-year-old comparison and 2 pairs were repeated for the 2-year-old versus 5-year-old comparison. Among those females that actually responded (see below), only 2 of the 8 pairs were represented twice in the 2-year-old versus 10-year-old comparison and none were represented twice in the 2-year-old versus 5-year-old comparison, making any concerns about pseudo-replication negligible.

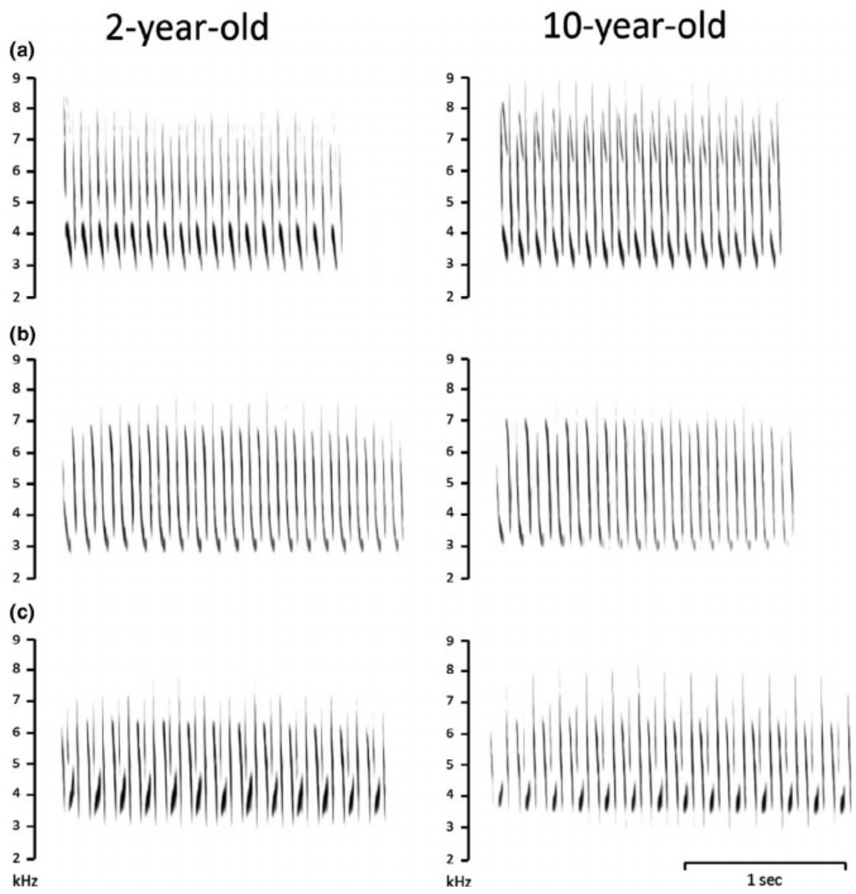

FIGURE 1 (a–c) Three examples of male songs recorded from the same males at different ages. Each pair includes one example of a song that a male sung when he was two years old (left) and a song of the same song type that he sung when he was 10 years old (right). Reproduced from Zipple et al. (2020)

Evidence suggests that these comparisons are ecologically relevant, although older males may be relatively rare in the population. The USGS bird longevity database contains five records of recaptured adult swamp sparrows. Of these five birds, two were known to be nearly eight years old at the time of recapture, and the *youngest* was nearly five years old (USGS, 2020). Thus, it seems likely that females will regularly encounter five-year-old males in this population and may occasionally encounter a ten-year-old male.

2.4 | Collection and hormonal treatment of females

We collected wild female swamp sparrows from Crawford County, PA, USA, during the 2020 breeding season. All birds were in breeding condition (as evidenced by the existence of a brood patch), but we could not determine their ages beyond the fact that they were at least one-year-old. We transported females to the laboratory in Durham, NC, and housed them in individual sound isolation chambers (Industrial Acoustics AC-1, 58 x 41 x 36 cm). After allowing females to become acclimated to the laboratory environment, we gave each individual a subcutaneous implant of 17-β-estradiol in silastic tubing (1.96 mm outer diameter), containing 7–9 mm of estrogen 9 days before we began copulation solicitation assays (following methods of Anderson, 2009; Ballentine et al., 2004; Searcy et al., 2002, 2010). This dosage is modeled on that found by Moore (1983) to produce plasma levels of estrogens in the normal range for females breeding in nature in the closely related white-crowned sparrow (Wingfield & Farner, 1978). We removed the implant at the conclusion of trials.

2.5 | Copulation solicitation assays

We measured the response of the estradiol-treated females to the song stimuli described above using the number of copulation solicitation displays performed as the sole response measure (King & West, 1977; Searcy, 1992). Each subject was tested with two pairs of contrasting stimuli: 1) Songs recorded from a 2-year-old male versus songs from the same male recorded as a 5-year-old, and 2) songs recorded from a different 2-year-old male versus songs from that male recorded as a 10-year-old.

On each day of testing, trials began in the morning at 30 with all acoustic chambers closed. Proceeding one female at a time, the door to one acoustic chamber was opened and the female in that chamber was played a set of 20 songs from one of the two pairs of stimuli listed above. Songs were played at an amplitude of 82dB SPL from an Advent Powered Partner Speaker AV570 placed 1 meter from the opening of the acoustic chamber. We recorded videos of females' responses to the songs. After playback of the 20 songs concluded, the door of the female's acoustic chamber was closed, and testing proceeded with the next female ($n = 12$ females total). Tests were repeated in the afternoon of each day, beginning at 1,430, with females hearing the second set of songs from the same stimulus pair they heard in the morning (i.e., birds that heard 2-year-old songs in the morning heard 5- or 10-year-old songs in the afternoon and vice versa, in a counter-balanced design). Two days later, trials were repeated with the same sets of stimuli, but the order of presentation of songs was reversed between the morning and the afternoon to control for differences in females' responsiveness across the day.

Beginning on June 15, birds' responses were measured on every other day in the following manner. On June 15 and June 17, all birds heard 2-year-old and 10-year-old songs, in the counter-balanced manner described above. Half of all birds ($n = 6$) heard the 2-year-old songs first, and the other half heard the 10-year-old songs first. On June 19 and June 21, half of the birds ($n = 6$) heard songs from 2-year-olds and 5-year-olds, while the other half participated in another experiment testing for female preferences for 1-year-old versus 2-year-old songs, not described here. Then, on June 23 and June 25, the final six birds heard songs from 2-year-olds and 5-year-olds.

2.6 | Inter-observer reliability

Playback experiments were watched and scored live by MNZ, and video recordings of the trials were scored by SN. Importantly, all scoring by both observers was done completely blind with respect to the treatment. During initial scoring, MNZ scored only the absence or presence of any copulation solicitation display in response to each song (i.e., 0/1) while SN scored total number of displays (with 0, 1, or 2 displays being observed per song). MNZ and SN agreed on presence/absence of displays for 98.9% of songs (2,847 out of 2,880). MNZ then re-scored those songs for which MNZ and SN disagreed as well as all songs where SN initially identified two displays. After this first revision of scores, MNZ and SN agreed on the number of displays given in response to 99.2% of songs (2,856 out of 2,880). SN then performed a final round of reconciliation, re-scoring the 24 songs where MNZ and SN disagreed. After this round of rescoring, MNZ and SN agreed in 99.7% of cases (2,871 out of 2,880). We resolved these final 9 disagreements by accepting the score of the more experienced observer (SN). Inter-observer reliability was therefore extremely high, even before any reconciliation, giving us confidence in the accuracy of our measures of female response.

2.7 | Statistical analyses

Because different birds heard songs from males of different ages at different times and on different days, all comparison of females' response are within-individual. The question of interest is whether birds responded more strongly to songs recorded from 2-year-old males as compared to songs recorded from the same males when they were five or ten years old.

To answer this question, we first counted the total number of displays that a female gave to each category of songs during a two-day set of trials (four total trials across two days). For example, if a bird displayed 12 times in the morning of June 15 (stimulus A), 14 times in the afternoon of June 15 (stimulus B), 16 times in the morning of June 17 (stimulus B), and 8 times in the afternoon of June 17 (stimulus A), she responded a total of 20 times to stimulus A (12 + 8) and 30 times to stimulus B (14 + 16). The data analyst (MNZ) was unblinded and allowed to know the ages of stimulus A and B only after all total responses were calculated.

We then performed paired *t* tests in R v3.5 (R Development Core Team, 2018) to determine whether females responded differently to (1) the 2-year-old stimuli as compared to the 10-year-old stimuli (using data collected on June 15 and June 17), and (2) the 2-year-old stimuli as compared to the 5-year-old stimuli (using data collected on June 19, 21, 23, and 25).

3 | RESULTS

In total, 9 of the 12 females performed at least one copulation solicitation display during the trials comparing 2-year-old and 10-year-old song. Six of the 12 did the same for the trials comparing 2-year-old and 5-year-old song. We included only these females in our analyses. It is uncommon for 100% of females to respond to playback of male songs in copulation solicitation assays, and this response rate is within the published range (reviewed in Searcy, 1992).

We found no evidence that females displayed significant preferences for any of our stimuli (Figure 2). Contrary to our prediction (https://aspredicted.org/zt3vh.pdf), females did not produce significantly more displays in response to songs recorded from males when they were 2 years old as compared to songs recorded from those males when they were either 10 years old (mean difference = 2.2 more displays given in response to the 2-year-old songs, *df* = 8, t = 0.82, *p* = .44) or 5 years old (difference = 2.0 more displays given in response to the 5-year-old songs, *df* = 5, t = 0.78, *p* = .47) years old.

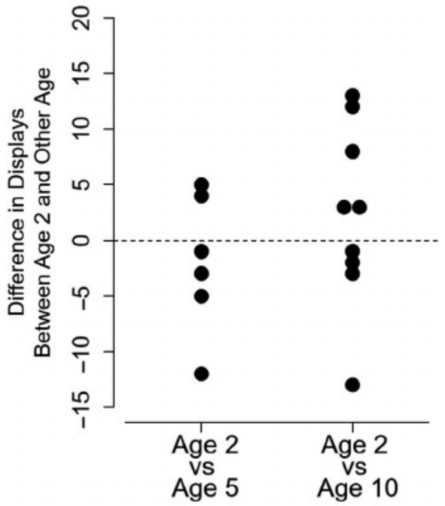

FIGURE 2 Receptive females do not display evidence that they discriminate within-individual vocal senescence. This figure shows the difference between the number of copulation solicitation displays that individual females gave when they heard songs recorded from a male when he was two years old compared to songs from the same male who was either 5 or 10 years old. Positive values would indicate a preference for the 2-year-old songs (our predicted result)

Of the nine birds that responded to the 2-year-old versus 10-year-old trials, 5 (56%) produced more displays when hearing the 2-year-old songs and 4 (44%) produced more when hearing the 10-year-old songs. Of the six birds that responded to the 2-year-old versus 5-year-old trials, 2 (33%) produced more displays when hearing the 2-year-old songs and 4 (67%) produced more when hearing the 5-year-old songs. Combining data for both comparisons, females produced more displays when hearing the 2-year-old songs in just 7 out of 15 trials (47%).

4 | DISCUSSION

Contrary to our predictions, we found no evidence that female swamp sparrows prefer songs recorded from peak-aged (2-year-old) males as compared to songs recorded from the same individuals when they were older males (5-year-olds) or even potentially highly senescent males (10-year-olds). These results are surprising because territorial males have been shown to attend to these within-individual declines in vocal quality (Zipple et al., 2020), and female birds in numerous species have been shown to be as discriminating or more discriminating than males in their responses to song (Searcy & Brenowitz, 1988; Searcy, 1990; Ratcliffe & Otter, 1996; Searcy et al., 2002; but see Nelson & Soha, 2004). In swamp sparrows, in particular, both females and males discriminate between songs that differ in how physically challenging they are to perform (Ballentine et al., 2004; DuBois et al., 2011).

What might explain why females do not appear to discriminate between the songs of peak-aged and senescent males? One reasonable possibility is that females do display discrimination between peak-aged and senescent males, but that our sample size (*n* = 9, 6) is too small to reliably return statistically significant results. We cannot exclude this possibility, but our sample sizes are in line with sample sizes (*n* = 6, 8, 10, 10) from previous studies in swamp sparrows and song sparrows that have used similar copulation solicitation display protocols to assess female preferences (Anderson, 2009; Ballentine et al., 2004; Searcy et al., 1981, 2010). In order for us to detect a significant result, given our sample size and the observed variance in this experiment, females would need to display a 43% increase in their responsiveness to 2-year-old songs as compared to 10-year-old songs or a 58% increase in their responsiveness to 2-year-old as compared to 5-year-old songs. These would represent substantial preferences, but they would be in line with previous results from this population. For example, Ballentine et al., 2004 found that females displayed a 42% increase in the number of displays that they gave to high-performance as compared to low-performance song and Anderson (2009) found that females produced 300% more displays in response to songs from their own population as compared to a different population. On the whole, our results in this study and in

Zipple et al. (2019) are consistent with those of Nelson and Soha (2004), who find that female white-crowned sparrows are less discriminating than males, at least along one axis of song variation.

If we assume that our results are not simply the result of a small sample size, but instead accurately reflect a lack of age-based preferences by females, what might explain such a result? It seems unlikely that females are *unable* to discriminate between the songs of peak-aged and senescent males. We have shown previously that territorial males respond differentially to age-related differences in the exact same playback stimuli that we used here. And, to the extent that we would expect selection to produce sex-specific differentiation of discrimination abilities, we would expect females to be under stronger selection to detect differences between songs as compared to males (Searcy & Brenowitz, 1988). This is because males and females should display different strategies in solving the problem of signal detection (Wiley, 2006). Males should respond to many potential threats, including some that are false alarms, because failing to respond to a territorial threat can be quite costly (i.e., discriminating between threats when no such discrimination was warranted, a Type 1 error), while females should be selected to respond more selectively to potential mates, because mating with a low-quality male can be quite costly (a failure to discriminate, a Type 2 error; Searcy & Brenowitz, 1988). Thus, although our data do not indicate that females differentially respond to males of different ages, we think it is unlikely that this is the result of simply being physiologically unable to do so.

A more likely possibility is that females are able to identify differences in singers' ages, but respond to all fully mature singers (> 2 years of age) in the same way, at least under the experimental conditions we used to test them. Female swamp sparrows are highly responsive to between-individual differences in males' ability to sing physically challenging songs (Ballentine et al., 2004), as measured by "deviation score" (a metric of vocal performance, which is the deviation of a male's performance from a maximum, physically constrained performance, Podos, 1997). Yet, deviation score was not related to age in our recorded males, but instead showed an extremely high level of within-individual repeatability from one year to the next (R = 0.93, Zipple et al., 2019). If females are attending primarily to differences in deviation score in assessing songs, then we would not expect them to respond to within-individual senescent changes in song, because this senescence does not appear to affect deviation score directly. This interpretation is consistent with the hypothesis that different vocal components or characteristics of songs have different functions for different receivers (Gil & Gahr, 2002; Kipper & Kiefer, 2010).

An adaptive scenario for why territorial males attend to age-related changes in song and reproductive females do not is as follows. As prospective mates, old males have both positive and negative attributes: On the positive side, they have demonstrated good genes for survival, whereas on the negative side, old males have accumulated germline mutations and may be less fertile. These positive and negative attributes should cancel each other out to some extent, so that the age of a prospective mate may not have much net effect on a female's fitness. Alternatively, females may prefer younger males as social mates, but older males as extra-pair mates (or *vice versa*), which could also lead to equivocal results under our testing paradigm. As territorial rivals, by contrast, old males have one attribute of overwhelming importance: They are behaviorally senescent, which makes them less formidable as competitors for territory. Consequently, females show no discrimination in a courtship context between songs of old and peak-aged males, whereas males do show discrimination in a territory defense context by giving a weaker response to the songs of old males. This scenario is speculative, but aspects of it should be testable.

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REFERENCES

Akçay, Ç., Arnold, J. A., Hambury, K. L., & Dickinson, J. L. (2016). Age-based discrimination of rival males in western bluebirds. *Animal Cognition*, *19*, 999–1006. https://doi.org/10.1007/s10071-016-1004-3

Anderson, R. C. (2009). Operant conditioning and copulation solicitation display assays reveal a stable preference for local song by female swamp sparrows *Melospiza georgiana*. *Behavioral Ecology and Sociobiology*, *64*, 215–223. https://doi.org/10.1007/s00265-009-0838-y

Ballentine, B., Hyman, J., & Nowicki, S. (2004). Vocal performance influences female response to male bird song: An experimental test. *Behavioral Ecology*, *15*, 163–168. https://doi.org/10.1093/beheco/arg090

Brooks, R., & Kemp, D. J. (2001). Can older males deliver the good genes? *Trends in Ecology & Evolution*, *16*, 308–313. https://doi.org/10.1016/S0169-5347(01)02147-4

Catchpole, C., & Slater, P. (2008). *Bird song: Biological themes and variations*, 2nd ed. Cambridge University Press.

Cucco, M., & Malacarne, G. (1999). Is the song of black redstart males an honest signal of status? *Condor*, *101*, 689–694. https://doi.org/10.2307/1370203

de Kort, S. R., Eldermire, E. R. B., Valderrama, S., Botero, C. A., & Vehrencamp, S. L. (2009). Trill consistency is an age-related assessment signal in banded wrens. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 2315–2321. https://doi.org/10.1098/rspb.2009.0127

Dean, R., Cornwallis, C. K., Løvlie, H., Worley, K., Richardson, D. S., & Pizzari, T. (2010). Male reproductive senescence causes potential for sexual conflict over mating. *Current Biology*, *20*, 1192–1196. https://doi.org/10.1016/J.CUB.2010.04.059

DuBois, A. L., Nowicki, S., & Searcy, W. A. (2011). Discrimination of vocal performance by male swamp sparrows. *Behavioral Ecology and Sociobiology*, *65*, 717–726. https://doi.org/10.1007/s00265-010-1073-2

DuVal, E. H. (2012). Variation in annual and lifetime reproductive success of lance-tailed manakins: Alpha experience mitigates effects of senescence on siring success. *Proceedings of the Royal Society B-Biological Sciences*, *279*, 1551–1559. https://doi.org/10.1098/rspb.2011.1840

Ferkin, M. H. (1999). Attractiveness of opposite-sex odor and responses to it vary with age and sex in meadow voles (*Microtus pennsylvanicus*). *Journal of Chemical Ecology*, *25*, 757–769. https://doi.org/10.1023/A:1020884431604

Gil, D., & Gahr, M. (2002). The honesty of bird song: Multiple constraints for multiple traits. *Trends in Ecology & Evolution*, *17*, 133–141.

Jones, T. M., Balmford, A., & Quinnell, R. J. (2000). Adaptive female choice for middle-aged mates in a lekking sandfly. *Proceedings of the Royal Society B-Biological Sciences*, *267*, 681–686. https://doi.org/10.1098/rspb.2000.1056

King, A. P., & West, M. J. (1977). Species identification in the North American cowbird: Appropriate responses to abnormal song. *Science*, *195*(4282), 1002–1004. https://doi.org/10.1126/science.841321

Kipper, S., & Kiefer, S. (2010). Age-related changes in birds' singing styles: On fresh tunes and fading voices? *Advances in the Study of Behaviour*, *41*, 77–118. https://doi.org/10.1016/S0065-3454(10)41003-7

Kokko, H. (1997). Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology*, *41*, 99–107. https://doi.org/10.1007/s002650050369

Kokko, H. (1998). Good genes, old age and life-history trade-offs. *Evolutionary Ecology*, *12*, 739–750. https://doi.org/10.1023/A:1006541701002

Lopez, P., Aragon, P., & Martin, J. (2003). Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflect their mating preference for older males. *Behavioral Ecology and Sociobiology*, *55*, 73–79. https://doi.org/10.1007/s00265-003-0675-3

Manning, J. T. (1985). Choosy females and correlates of male age. *Journal of Theoretical Biology*, *116*, 349–354. https://doi.org/10.1016/S0022-5193(85)80273-3

Moore, M. C. (1983). Effect of female sexual displays on the endocrine physiology and behaviour of male white-crowned sparrows, *Zonotrichia leucophrys*. *Journal of Zoology*, *199*, 137–148. https://doi.org/10.1111/j.1469-7998.1983.tb02085.x

Nelson, D., & Soha, J. (2004). Male and female white-crowned sparrows respond differently to geographic variation in song. *Behaviour*, *141*, 53–69. https://doi.org/10.1163/156853904772746600

Nussey, D. H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M., & Austad, S. N. (2013). Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, *12*, 214–225. https://doi.org/10.1016/J.ARR.2012.07.004

O'Loghlen, A. L., & Rothstein, S. I. (2003). Female preference for the songs of older males and the maintenance of dialects in brown-headed cowbirds (*Molothrus ater*). *Behavioral Ecology and Sociobiology*, *53*, 102–109. https://doi.org/10.1007/s00265-002-0551-6

Pizzari, T., Dean, R., Pacey, A., Moore, H., & Bonsall, M. B. (2008). The evolutionary ecology of pre- and post-meiotic sperm senescence. *Trends in Ecology & Evolution*, *23*, 131–140. https://doi.org/10.1016/J.TREE.2007.12.003

Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (*Passeriformes: Emberizidae*). *Evolution (N Y)*, *51*, 537–551. https://doi.org/10.1111/j.1558-5646.1997.tb02441.x

R Development Core Team (2018) *R: a language and environment for statistical computing*. Vienna, Austria: R Development Core Team.

Ratcliffe, L., & Otter, K. (1996). Sex differences in song recognition. In D. Kroodsma, & E. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 339–355). Cornell University Press.

Searcy, W. A. (1990). Species recognition of song by female red-winged blackbirds. *Animal Behavior*, *40*, 1119–1127. https://doi.org/10.1016/S0003-3472(05)80178-2

Searcy, W. A. (1992). Measuring responses of female birds to male song. In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 175–189). Springer.

Searcy, W. A., & Brenowitz, E. A. (1988). Sexual differences in species recognition of avian song. *Nature*, *332*, 152–154. https://doi.org/10.1038/332152a0

Searcy, W. A., Marler, P., & Peters, S. S. (1981). Species song discrimination in adult female song and swamp sparrows. *Animal Behavior*, *29*, 997–1003. https://doi.org/10.1016/S0003-3472(81)80053-X

Searcy, W. A., & Nowicki, S. (2005). *The evolution of animal communication: Reliability and deception in signaling systems*. Princeton University Press.

Searcy, W. A., Nowicki, S., Hughes, M., & Peters, S. (2002). Geographic song discrimination in relation to dispersal distances in song sparrows. *American Naturalist*, *159*, 221–230. https://doi.org/10.1086/338509

Searcy, W. A., Peters, S., Kipper, S., & Nowicki, S. (2010). Female response to song reflects male developmental history in swamp sparrows. *Behavioral Ecology and Sociobiology*, *64*, 1343–1349. https://doi.org/10.1007/s00265-010-0949-5

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Cambell (Ed.), *Sexual selection and the descent of man 1871–1971* (pp. 139–179). Aldine.

United States Geological Survey (USGS) (2020). Longevity records of North American birds. Retrieved from: https://www.pwrc.usgs.gov/BBL/longevity/Longevity_main.cfm

Wiley, R. H. (2006). Signal detection and animal communication. *Advances in the Study of Behaviour*, *36*, 217–247. https://doi.org/10.1016/S0065-3454(06)36005-6

Wingfield, J. C., & Farner, D. S. (1978). The annual cycle of plasma irLH and steroid hormones in feral populations of the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. *Biology of Reproduction*, *19*, 1046–1056. https://doi.org/10.1095/biolreprod19.5.1046

Zipple, M. N., Nowicki, S., Searcy, W. A., & Peters, S. (2019). Full life course analysis of birdsong reveals maturation and senescence of highly repeatable song characteristics. *Behavioral Ecology*, *30*, 1761–1768. https://doi.org/10.1093/beheco/arz146

Zipple, M. N., Peters, S., Searcy, W. A., & Nowicki, S. (2020). Sounds of senescence: Male swamp sparrows respond less aggressively to the songs of older individuals. *Behavioral Ecology*, *31*, 533–539. https://doi.org/10.1093/beheco/arz218

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