Tuning and fading voices in songbirds: age-dependent changes in two acoustic traits across the life span

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Age-related phenotypic changes (maturation–senescence) commonly occur during an organism's lifetime. While maturation is usually considered as a measure of individual quality, senescence is associated with loss of function and physiological deterioration. To date, little is known about age-dependent expression of acoustic sexually selected traits over a lifetime. Using a free-living population of great tits, *Parus major*, we recorded the song of individually marked males in a standardized way during a 4-year period, in a longitudinal design. The study focused on two previously identified, acoustic, sexually selected signals: song consistency and repertoire size. Young (1–2 years old) and old (5–6 years old) individuals expressed lower song consistency than individuals at intermediate age (3–4 years old), suggesting song tuning during the first 3 years of life, and deterioration after the peak is reached. Repertoire size, in contrast, did not vary with age. To the best of our knowledge, our study is the first to evaluate song changes at advanced age and to report senescence effects on song expression in free-living songbirds. Our results suggest that, similarly to speech in humans, different aspects of birdsong are differentially affected by age: while motor performance traits (song consistency) deteriorate with age, language skills (repertoire size) may not be affected during the life span.

Organisms change permanently during their lifetime, displaying age-related variation in various morphological, life history and sexually selected traits (Monaghan et al. 2008). These changes are mainly the result of two different processes. First, there are age-dependent phenotypic changes that involve development or maturation (Monaghan et al. 2008). Second, there is physiological deterioration also known as ageing or senescence (Kirkwood & Austad 2000; Monaghan et al. 2008). While the first is usually considered a measure of individual quality (Andersson 1994), the latter is associated with loss of function, decrease in reproduction and an increase in mortality (Kirkwood & Austad 2000; Monaghan et al. 2008). Studying the evolutionary mechanisms behind these two age-related processes is of extreme interest, and has drawn researchers' attention to acquiring an understanding of how age-related changes are controlled and whether these processes have any fitness consequences (Monaghan et al. 2008; Evans et al. 2011).

Age-related changes have been studied using two different approaches. In the first approach, which is known as a cross-sectional study, each individual is sampled only once (Nussey et al. 2008). Although this method enables data collection in a single year, it excludes within-individual variation, and may be biased by differential mortality (Endler 1986; Nussey et al. 2008). The second method involves the collection of repeated data at different ages from the same individuals. This approach, known as a longitudinal study, provides a more reliable estimation of within-individual age-related changes (Nussey et al. 2008). However, this approach is not commonly applied, since the collection of field data across several years may be labour intensive, making it more difficult to obtain comprehensive data sets suitable for analysis.

Sexual selection theory suggests that certain attributes (sexually selected traits) may evolve by mate preference or as the result of direct competition between males to have access to females (Darwin 1871; Andersson 1994). Age-dependent expression of sexually selected traits has been reported in a wide variety of taxa (Johnstone 1995). Studies on senescence have mainly focused on life history characteristics and mortality (Williams et al. 2006; Jones et al. 2008), while studies on ageing of secondary sexual traits have received less attention (Williams et al. 2006). Because allocation of resources for reproduction may have an impact on survival owing to life history trade-offs (Kirkwood 2001; Monaghan et al. 2008), sexually selected traits may show not only maturation, but also a senescent effect (Evans et al. 2011). Therefore, the incorporation of sexual selection into senescence studies may greatly contribute to our understanding of the ageing process (Bonduriansky et al. 2008).

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Birdsong is a well-known sexually selected trait, which has been found to play a fundamental role in both mate attraction and intrasexual interactions (Catchpole & Slater 2008). Given that birdsong has been found to provide reliable information about individual quality (Catchpole & Slater 2008), birdsong production (memorization, development, output) may require large allocation of resources (Gil & Gahr 2002). Theoretically, birdsong expression may vary in relation to age in two different directions. First, it may increase with age (Andersson 1994) as a result of gained experience, learning or late maturation (Garamszegi et al. 2007; Kipper & Kiefer 2010). Second, owing to life history trade-offs, allocation of resources to enhance the expression of a sexually selected trait may have an impact on later allocation to somatic repair and survival (Kirkwood & Austad 2000; Kokko et al. 2002), which may cause physical and physiological deterioration of the trait at old age (Bonduriansky et al. 2008). Although age-dependent expression of birdsong has been extensively studied (Kipper & Kiefer 2010), most of these studies have only considered song repertoire size as a measure of individual quality (Kipper & Kiefer 2010), and little is known regarding age-related changes in song-structural traits. Moreover, in spite of the large number of studies on age-related changes in the expression of birdsong (Kipper & Kiefer 2010), the effects of senescence on birdsong are largely unknown.

To achieve a better understanding of the effects that maturation and senescence processes may have on birdsong across a lifetime, we designed a longitudinal study in a wild population of the great tit, *Parus major*, a widely used model species. Previous studies investigating senescence in great tits have focused on females (Bouwhuis et al. 2010, 2012). However, by studying birdsong, a well-studied male characteristic, we can assess age-dependent changes (maturation–senescence) of a sexually selected trait in males. We therefore studied within-individual variation in expression of two acoustic traits to investigate whether expression of a well-known sexually selected trait increases (maturation) and/or decreases (senescence) during the life span in great tit males. In addition, by studying two different traits, we wanted to investigate whether the traits follow a similar or a divergent pattern of change in expression with age. We followed individually colour-ringed males over a 4-year period, including individuals between 1 and 6 years of age, covering stages from yearling until maximum expected life span in our population. During the study, we collected song recordings in a systematic and standardized manner, taking into account the singing ecology of the species (Rivera-Gutierrez et al. 2010, 2011a). As a previous cross-sectional study in this species suggested that song consistency, a structural trait, may vary with age, and repertoire size may be associated with survival (Rivera-Gutierrez et al. 2010), our analysis focused on these two acoustic characteristics.

METHODS

Ethical Note

The study was approved by the ethical committee of the University of Antwerp (ID number 2006/22) and it was performed in accordance with Belgian and Flemish law. The Belgian Royal Institute for Natural Sciences (Koninklijk Belgisch Instituut voor Natuurwetenschappen) provided ringing licences for authors and technical personnel. The methods that we used (song recording, nest checking, ringing) created only a very low level of stress that did not cause any desertion or nestling mortality.

Study Area and General Procedures

Great tits are cavity breeders that readily accept nestboxes for breeding in spring and roosting during winter. We collected data between spring 2007 and spring 2010 from a resident, suburban, nestbox population located at the campus Drie Eiken of the University of Antwerp, Belgium. This population is monitored year round: all individuals are metal-ringed as nestlings or when first caught, and adults receive a combination of three colour rings, to enable individual identification. All great tits are caught at the nest by using standardized protocols. Adult great tits are caught while roosting at night during winter or while feeding nestlings and only when nestlings are at least 8 days old. Nestlings are ringed when they are at least 10 days old. Exact age in years was determined by using hatching records for resident birds, and by using colour differences for primary coverts for yearling birds that did not hatch in the nestboxes of our population (Rivera-Gutierrez et al. 2010). The present study only includes individuals of known age that stayed in the population for at least two breeding periods.

Song Recordings and Analysis

Great tit males sing uninterruptedly in the surroundings of the nest at dawn throughout the reproductive period, showing a peak during egg laying (Mace 1987). This display is known as the dawn chorus, and when fully recorded, it has been shown to provide a repeatable estimation of the song repertoire (Van Duyse et al. 2005; Rivera-Gutierrez et al. 2011a). All recordings were collected in a standardized way during the 4-year period. We only recorded and considered for analysis the complete dawn chorus of individually marked great tit males during the egg-laying period of their females (Rivera-Gutierrez et al. 2011a). Special care was taken to arrive before the males started singing, and the end of the dawn chorus was taken to be when the female emerged from the nest and often engaged in copulation with the male (Mace 1987; Rivera-Gutierrez et al. 2010, 2011a). A Sennheiser Me67/K6 microphone attached to a portable Marantz PMD660 solid-state digital recorder was used to record the individuals manually at an approximate distance of 20 m, or an M-Audio (MicroTrack 24/96 or MicroTrack II) Professional Mobile Digital Recorder was placed on top of the nestbox. Recording settings were the same for both recorders: PCM, 44100 Hz, 16 Bit, Mono (Rivera-Gutierrez et al. 2010, 2011a).

Song recordings were submitted to spectrographic analysis by using Avisoft-SAS Labpro 4.5 (Avisoft, Berlin, Germany; sonogram parameters: Hamming window, fast Fourier transform length 256, frame size 75% and overlap of 50%). All different song types per individual were identified and a library was constructed to establish repertoire composition and enabling comparison of repertoire size between years (Rivera-Gutierrez et al. 2010, 2011a). The total number of different song types in a single dawn chorus was considered as the repertoire size in a particular year per individual (Rivera-Gutierrez et al. 2010, 2011a).

Song consistency was assessed by means of average spectrographic cross-correlation (SPCC; Clark et al. 1987), which has previously been found to reflect the structural similarity of the analysed songs accurately (Botero et al. 2009; Rivera-Gutierrez et al. 2010, 2011b). Based on a good signal-to-noise ratio, 30 consecutive or semiconsecutive phrases per song type were chosen from the same song bout. By using Avisoft-SAS Labpro 4.5, we created individual spectrograms of the same duration from the chosen phrases per song type (Rivera-Gutierrez et al. 2010). All different spectrograms per song type were uploaded into Avisoft-Correlator (version 2.2 2008), which performed a pairwise comparison of frequency and duration parameters to establish the SPCC. Values per song type were used to calculate average values per individual, while controlling for the number of song types (Rivera-Gutierrez et al. 2010).

Statistical Analysis

Data were analysed by using linear mixed-effect models (LMM), which allow longitudinal analysis (within-individual variation), while controlling for nonindependence of repeated data (Nussey et al. 2008). In our model, individuals were set as subject and age as repeat. Age in years was fitted as a linear as well as quadratic factor, to test for nonlinear effects. We also included the last observed age in years (LA) as a factor to analyse a possible effect of longevity (Evans et al. 2011). Year was included as a factor to control for the possible effects of between-year variation. Individuals were included as a random factor to control for nonindependence of repeated data. Age, Age^2, LA and Year were included as fixed factors. As song consistency was calculated as the average from all different song types per individual, this model also included repertoire size as a factor. We followed a backward stepwise elimination procedure to exclude nonsignificant terms (>0.1) and to achieve the minimum adequate models. All analyses were performed in JMP 9.0 for Mac (SAS Institute Inc., Cary, NC, U.S.A.) and figures were made with Sigmaplot for Windows version 8.02 (Systat Software Inc., San Jose, CA, U.S.A.).

RESULTS

A total of 104 complete dawn choruses from 45 individual males were obtained over a period of 4 years (2007–2010). The number of dawn choruses obtained per individual ranged between two and four (mean ± SE = 2.31 ± 0.08). The age of the males varied between 1 and 6 years old, covering all stages from yearling up until maximum expected life span in our population. Dawn choruses were collected from individuals in all age stages. A total of 15 dawn choruses were collected from males that were 1 year old, 34 from 2-year-old males, 27 from 3-year-old males, 15 from 4-year-old males, 10 from 5-year-old males and three from 6-year-old males. A total of 33 males were followed over a 2-year period, 10 over a 3-year period and two over a 4-year period.

Age and Age^2 significantly predicted song consistency (Table 1), showing a pattern of increased song consistency from year 1 until year 3–4, when a plateau was reached (Fig. 1a). A quadratic function was the best predictor of variation, suggesting that the turning point is when birds are about 3.5 years old, when song consistency started to decrease (Fig. 1a). Repertoire size did not contribute to explain song consistency and was, therefore, excluded (Table 1). Similarly, LA (longevity) did not have a significant contribution in the model, and was also removed (Table 1). The model showed that year of sampling had a marginally significant effect on song consistency (Table 1). This effect may be the result of clustering of age classes per year, or because the last year (2010) did not include males that were 1 year old. An additional model excluding Year as a factor shows that the effect of Age and Age^2 is still highly significant (Age: $F_{1,79.98} = 47.35$, $P < 0.0001$; Age^2: $F_{1,75.31} = 41.24$, $P < 0.0001$) suggesting that year of sampling did not affect the general model, and by including year as a factor we consider the
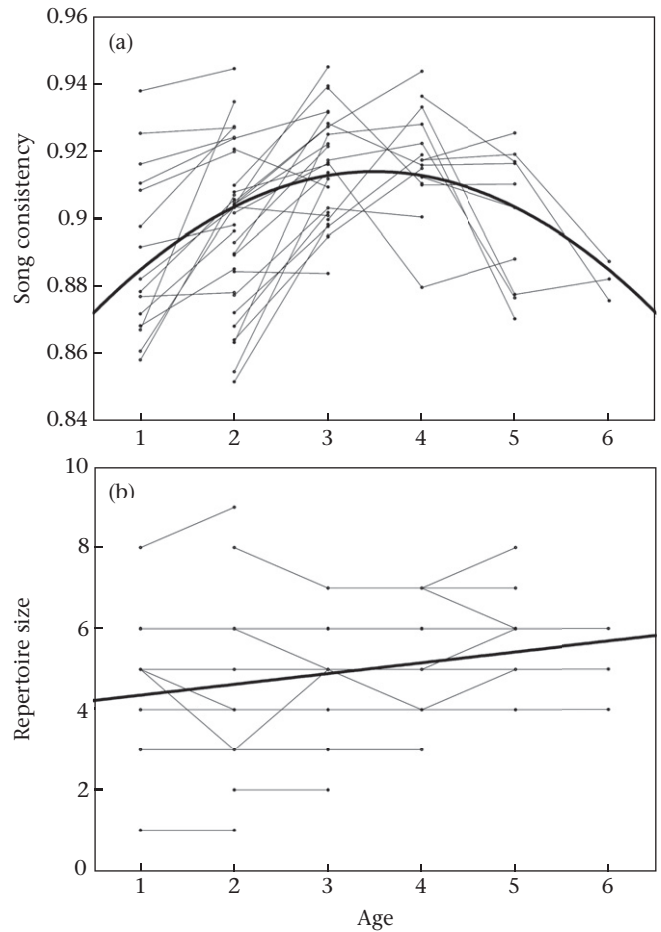

Figure 1. Within-individual variation of (a) song consistency and (b) repertoire size, as a function of age. Thinner lines represent within-individual variation between years. Thicker lines show the general model that best describes the variation: (a) quadratic model: $R^2 = 0.19$; (b) linear model: $R^2 = 0.05$. The sample size is the same ($N = 45$) for both song parameters (song consistency and repertoire size), but because males may have a similar repertoire size or song consistency value there seem to be fewer individuals.

variance associated with it. In contrast to song consistency, repertoire size did not vary as a factor of Age, Age^2 or Year (Table 1, Fig. 1b), although some males added or dropped song types between years. However, LA showed a nonsignificant positive trend with repertoire size, suggesting that individuals that live longer have a larger song repertoire (Table 1).

DISCUSSION

Our longitudinal analysis provides evidence for the various effects that age-dependent change and longevity have on two

Table 1
Linear mixed model of within-individual variation of song consistency and repertoire size

Factor	Song consistency					E	Repertoire size					E
	Estimate	SE	df	F ratio	Prob>F		Estimate	SE	df	F ratio	Prob>F	
LA	−0.003	0.004	1, 45.62	0.35	0.557	1	**0.328**	**0.168**	**1, 42.85**	**3.80**	**0.058***	
Year	**0.005**	**0.002**	**1, 80.29**	**2.22**	**0.03**		0.059	0.322	1, 42.02	0.03	0.85	1
Age	**0.006**	**0.002**	**1, 51.78**	**8.79**	**0.005**		−0.053	0.056	1, 58.26	0.91	0.345	3
Age^2	**−0.006**	**0.0009**	**1, 76.86**	**42.69**	**<0.001**		0.018	0.024	1, 58.97	0.74	0.463	2
Repertoire size	−0.002	0.002	1, 50.37	1.29	0.26	2						

LA: the last age at which observations were made for an individual. Column labelled E indicates order of exclusion. Text in bold indicates significant results, while text in bold in combination with * indicates a nonsignificant trend.

acoustic traits. First, the data revealed a differential expression of song consistency with age, showing that young (1−2 years old) and old (5−6 years old) birds expressed lower consistency, compared to birds at intermediate ages (3−4 years old), when the maximum expression of consistency was achieved. Our study is the first to report senescence effects on song expression in free-living birds. Second, repertoire size did not vary with age, but showed a nonsignificant positive trend with longevity, suggesting that males that live longer have a larger repertoire. Both results are in accordance with previous cross-sectional studies in the same population (Rivera-Gutierrez et al. 2010, 2011a).

Great Tits Tune their Song

The observed pattern of increasing song consistency during the first 3 years of life in the great tit is in accordance with previous studies regarding age-dependent expression of this song-structural trait in songbirds (Sakata & Vehrencamp 2012), suggesting that great tits tune their song during this time. Song consistency is a structural trait that requires the development of controlled motor abilities for syrinx and beak movements (Podos et al. 2009; Sakata & Vehrencamp 2012). Sensorimotor learning and practice, therefore, may help to increase consistency and tune the song. This stereotypic repetition of songs is likely to play a fundamental role in signalling the age of the singer during both inter- and intrasexual interactions. In an intersexual context song consistency has been found to correlate with extrapair paternity (Byers 2007), which may confirm its potential as a motor skill for influencing females' preferences (Byers et al. 2010). At present we do not have evidence that song consistency plays a role during female choice in the great tit. Remarkably, we observed that the peak of song consistency is achieved when birds are 3 years old, coinciding with the peak of females' reproductive success (Bouwhuis et al. 2009, 2010). This may suggest that the timing of peak performance is very similar in both sexes. From an intrasexual perspective, song consistency is known to signal age and dominance in tropical mockingbirds, *Mimus polyglottos*, and banded wrens, *Pheugopedius pleurostictus* (Sakata & Vehrencamp 2012). Experimental data have revealed that differences in song consistency are salient to great tit males during territorial encounters (Rivera-Gutierrez et al. 2011b), indicating that this trait may provide reliable information on age and dominance in this species, playing a fundamental role in territorial defence.

Great tit Song Fades at Older Age

Studies investigating age-related expression of acoustic traits have only revealed general patterns of increased expression or no change with age (Kipper & Kiefer 2010). Two previous studies in captive songbirds found that the expression of acoustic traits seems to decrease during adulthood, which may suggest a senescent effect. First, repertoire size in female European starlings, *Sturnus vulgaris*, decreased with age (Pavlova et al. 2010), suggesting that maintaining large repertoires may be costly for older females. During this study females of different age were grouped in only two age categories, and the entire life span was not covered. Second, in a study of Bengalese finches, *Lonchura striata domestica*, it was found that the expression of song tempo and frequency decreased in older individuals, while syllable repertoire size remained constant (Cooper et al. 2012). Although this study included individuals at the end of the life span, the sample size was very low (four individuals only), which decreases the power of the results. Our study on a free-living population and with a large number of individuals suggests that song consistency fades when individuals become older than 3 years of age. During our study, 27 individuals

out of 45 were sampled when maximum consistency was achieved (3 years of age), and 15 individuals were sampled at the age of 4 years, suggesting that our findings are not affected by a low sample size at older age. Our results are consistent with trade-offs in the expression of other sexually selected traits, in which older individuals show lower expression than individuals at intermediate age (Bonduriansky et al. 2008; Monaghan et al. 2008; Balbontin et al. 2011; Preston et al. 2011). Larger allocation of resources for overexpression may affect later allocation for somatic repair, which may cause physical and physiological deterioration (Kirkwood & Austad 2000; Hunt et al. 2004; Bonduriansky et al. 2008). As song consistency has been found to play a role both in sexual selection influencing female preferences (Byers 2007) and during intrasexual encounters (Botero et al. 2009; Rivera-Gutierrez et al. 2011b), it is possible that reduced expression of song consistency at older ages has fitness consequences, perhaps reducing extrapair paternity and/or decreasing the ability to defend territories.

Birdsong, as a complex acoustic signal, shares many characteristics with human speech (Doupe & Kuhl 1999). This striking similarity provides an interesting reference to understand senescence of acoustic characteristics in birds. In humans, different acoustic structural traits have been found to change in adult voice at old age. For instance, fundamental frequency may increase in men, while speech rate may decrease in general for men and women (Linville 1996; Torre & Barlow 2009). These changes are mainly attributed to anatomical and physiological changes in the vocal cord and respiratory system, decreased motor control and slower cognitive processing (Linville 1996; Torre & Barlow 2009). In great tits, song consistency, as a structural trait, may be constrained by sensorimotor learning (Podos et al. 2009; Sakata & Vehrencamp 2012), brain integrity (Botero et al. 2009), auditory feedback (Tumer & Brainard 2007), coordination of the respiratory system and development of motor abilities for syrinx and beak movements (Doupe & Kuhl 1999; Podos et al. 2009). One possible mechanism explaining senescence in acoustic traits in birds is atrophy of syrinx musculature caused by ageing, which may affect vocal motor performance (Linville 1996). A second explanation is that changes in the respiratory system and reduced elasticity in lung tissue, caused by ageing, may lower singing rate in older individuals (Linville 1996). This may cause a slowdown effect on the song, affecting its stereotypical repetition. An alternative explanation is that age-related neurological deterioration at the avian basal ganglia may affect motor abilities (Cooper et al. 2012) causing decreased consistency.

Repertoire Size does not vary with Age

Repertoire size, on the other hand, was not affected by age, confirming previous studies in this species (Rivera-Gutierrez et al. 2010, 2011a). Although some changes between years were observed, it is possible that underestimation of the repertoire becomes a confounding factor while doing field recordings (Rivera-Gutierrez et al. 2011a). Previous studies investigating senescence under laboratory conditions or conducted while studying free-living populations have suggested that senescence rate may differ between traits (Rueppell et al. 2007; Nussey et al. 2009), which may help to explain our results. On the other hand, birdsong repertoire may also offer a parallel with human speech, since sound organization in birdsong repertoires may resemble human rules for organizing words in a sentence (Doupe & Kuhl 1999). In humans, old adults have been found to perform similar or better than younger individuals in constructing sentences and having a coherent semantic structure (Miller & Johnson 2004). This suggests that senescence may not affect the syntactic structure and repertoire of birdsong, which may be controlled by brain integrity at the avian vocal centre (Garamszegi

& Eens 2004; Nottebohm 2005), whereas phonological abilities, which are based on motor performance, may deteriorate with age. We also observed a positive trend between repertoire size and longevity, which suggests that repertoire size may provide information on survival probability (Lambrechts & Dhondt 1986). It is possible then that repertoire size is signalling stress suffered during early development (Gorissen et al. 2005; Bischoff et al. 2009; Rivera-Gutierrez et al. 2010). As song acquisition probably occurs at an early age in great tits, environmental or nutritional stress suffered at such a stage may have a potential carryover effect, hampering song memorization and negatively affecting repertoire size (Rivera-Gutierrez et al. 2010).

Acknowledgments

References

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Balbontin, J., de Lope, F., Hermosell, I. G., Mousseau, T. A. & Møller, A. P. 2011. Determinants of age-dependent change in a secondary sexual character. *Journal of Evolutionary Biology*, **24**, 440–448.

Bischoff, L. L., Tschirren, B. & Richner, H. 2009. Long-term effects of early parasite exposure on song duration and singing strategy in great tits. *Behavioral Ecology*, **20**, 265–270.

Bondurianzky, R., Maklakov, A., Zajitschek, F. & Brooks, R. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. *Functional Ecology*, **22**, 443–453.

Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., de Kort, S. R. & Vehrencamp, S. L. 2009. Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. *Animal Behaviour*, **77**, 701–706.

Bouwhuis, S., Sheldon, B. C., Verhulst, S. & Charmantier, A. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proceedings of the Royal Society B*, **276**, 2769–2777.

Bouwhuis, S., van Noordwijk, A. J., Sheldon, B. C., Verhulst, S. & Visser, M. E. 2010. Similar patterns of age-specific reproduction in an island and mainland population of great tits *Parus major*. *Journal of Avian Biology*, **41**, 615–620.

Bouwhuis, S., Choquet, R., Sheldon, B. C. & Verhulst, S. 2012. The forms and fitness cost of senescence: age-specific recapture, survival, reproduction, and reproductive value in a wild bird population. *American Naturalist*, **179**, E15–E27.

Byers, B. E. 2007. Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behavioral Ecology*, **18**, 130–136.

Byers, J., Hebets, E. & Podos, J. 2010. Female mate choice based upon male motor performance. *Animal Behaviour*, **79**, 771–778.

Catchpole, C. K. & Slater, P. J. B. 2008. *Bird Song Biological Themes and Variations*. 2nd edn. Cambridge: Cambridge University Press.

Clark, C. W., Marler, P. & Beeman, K. 1987. Quantitative analysis of animal vocal phonology: an application to swamp sparrow song. *Ethology*, **76**, 101–115.

Cooper, B. G., Méndez, J. M., Saar, S., Whetstone, A. G., Meyers, R. & Goller, F. 2012. Age-related changes in the Bengalese finch song motor program. *Neurobiology of Aging*, **33**, 564–568.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: Murray.

Doupe, A. J. & Kuhl, P. K. 1999. Birdsong and human speech: common themes and mechanisms. *Annual Review of Neuroscience*, **22**, 567–631.

Endler, J. A. 1986. *Natural Selection in the Wild*. Princeton, New Jersey: Princeton University Press.

Evans, S. R., Gustafsson, L. & Sheldon, B. C. 2011. Divergent patterns of age-dependence in ornamental and reproductive traits in the collared flycatcher. *Evolution*, **65**, 1623–1636.

Garamszegi, L. Z. & Eens, M. 2004. Brain space for a learned task: strong intraspecific evidence for neural correlates of singing behavior in songbirds. *Brain Research Reviews*, **44**, 187–193.

Garamszegi, L. Z., Torok, J., Hegyi, G., Szollosi, E., Rosivall, B. & Eens, M. 2007. Age-dependent expression of song in the collared flycatcher, *Ficedula albicollis*. *Ethology*, **113**, 246–256.

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

Gorissen, L., Snoeijs, T., Van Duyse, E. & Eens, M. 2005. Heavy metal pollution affects dawn singing behaviour in a small passerine bird. *Oecologia*, **145**, 504–509.

Hunt, J., Brooks, R., Jennions, M. D., Smith, M. J., Bentsen, C. L. & Bussiere, L. F. 2004. High-quality male field crickets invest heavily in sexual display but die young. *Nature*, **432**, 1024–1027.

Johnstone, R. A. 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biological Reviews of the Cambridge Philosophical Society*, **70**, 1–65.

Jones, O. R., Gaillard, J. M., Tuljapurkar, S., Alho, J. S., Armitage, K. B., Becker, P. H., Bize, P., Brommer, J., Charmantier, A., Charpentier, M., et al. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecology Letters*, **11**, 664–673.

Kipper, S. & Kiefer, S. 2010. Age-related changes in birds' singing styles: on fresh tunes and fading voices? In: *Advances in the Study of Behavior* Vol. 41 (Ed. by H. J. Brockmann, T. J. Roper, M. Naguib, K. E. Wynne-Edwards, J. C. Mitani & W. S. Leigh), pp. 77–118 San Diego: Elsevier Academic Press.

Kirkwood, T. B. L. 2001. Sex and ageing. *Experimental Gerontology*, **36**, 413–418.

Kirkwood, T. B. L. & Austad, S. N. 2000. Why do we age? *Nature*, **408**, 233–238.

Kokko, H., Brooks, R., McNamara, J. M. & Houston, A. I. 2002. The sexual selection continuum. *Proceedings of the Royal Society B*, **269**, 1331–1340.

Lambrechts, M. & Dhondt, A. A. 1986. Male quality, reproduction, and survival in the great tit (*Parus major*). *Behavioral Ecology and Sociobiology*, **19**, 57–63.

Linville, S. E. 1996. The sound of senescence. *Journal of Voice*, **10**, 190–200.

Mace, R. 1987. The dawn chorus in the great tit *Parus major* is directly related to female fertility. *Nature*, **330**, 745–746.

Miller, M. D. & Johnson, J. S. 2004. Phonological and lexical-semantic short-term memory and their relationship to sentence production in older adults. *Aging Neuropsychology and Cognition*, **11**, 395–415.

Monaghan, P., Charmantier, A., Nussey, D. H. & Ricklefs, R. E. 2008. The evolutionary ecology of senescence. *Functional Ecology*, **22**, 371–378.

Nottebohm, F. 2005. The neural basis of birdsong. *PloS Biology*, **3**, 759–761.

Nussey, D. H., Coulson, T., Festa-Bianchet, M. & Gaillard, J. M. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology*, **22**, 393–406.

Nussey, D. H., Kruuk, L. E. B., Morris, A., Clements, M. N., Pemberton, J. M. & Clutton-Brock, T. H. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. *American Naturalist*, **174**, 342–357.

Pavlova, D. Z., Pinxten, R. & Eens, M. 2010. Age-related changes of song traits in female European starlings (*Sturnus vulgaris*). *Animal Biology*, **60**, 43–59.

Podos, J., Lahti, D. C. & Moseley, D. L. 2009. Vocal performance and sensorimotor learning in songbirds. In: *Advances in the Study of Behavior* Vol. 40 (Ed. by M. Naguib & V. M. Janik), pp. 159–195. Burlington: Elsevier Academic Press.

Preston, B. T., Jalme, M. S., Hingrat, Y., Lacroix, F. & Sorci, G. 2011. Sexually extravagant males age more rapidly. *Ecology Letters*, **14**, 1017–1024.

Rivera-Gutierrez, H. F., Pinxten, R. & Eens, M. 2010. Multiple signals for multiple messages: great tit, *Parus major*, song signals age and survival. *Animal Behaviour*, **80**, 451–459.

Rivera-Gutierrez, H. F., Pinxten, R. & Eens, M. 2011a. Difficulties when assessing birdsong learning programmes under field conditions: a re-evaluation of song repertoire flexibility in the great tit. *PLoS ONE*, **6**, e16003.

Rivera-Gutierrez, H. F., Pinxten, R. & Eens, M. 2011b. Songs differing in consistency elicit differential aggressive response in territorial birds. *Biology Letters*, **7**, 339–342.

Rueppell, O., Christine, S., Mulcrone, C. & Groves, L. 2007. Aging without functional senescence in honey bee workers. *Current Biology*, **17**, R274–R275.

Sakata, J. T. & Vehrencamp, S. L. 2012. Integrating perspectives on vocal performance and consistency. *Journal of Experimental Biology*, **215**, 201–209.

Torre, P. & Barlow, J. A. 2009. Age-related changes in acoustic characteristics of adult speech. *Journal of Communication Disorders*, **42**, 324–333.

Tumer, E. C. & Brainard, M. S. 2007. Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. *Nature*, **450**, 1240–1244.

Van Duyse, E., Pinxten, R., Snoeijs, T. & Eens, M. 2005. Simultaneous treatment with an aromatase inhibitor and an anti-androgen decreases the likelihood of dawn song in free-living male great tits, *Parus major*. *Hormones and Behavior*, **48**, 243–251.

Williams, P. D., Day, T., Fletcher, Q. & Rowe, L. 2006. The shaping of senescence in the wild. *Trends in Ecology & Evolution*, **21**, 458–463.