Ethology

First-Year Common Nightingales (*Luscinia megarhynchos*) Have Smaller Song-Type Repertoire Sizes Than Older Males

Sarah Kiefer*, Anne Spiess*†, Silke Kipper*, Roger Mundry*‡, Christina Sommer*, Henrike Hultsch* & Dietmar Todt*

* Institute of Biology, Behavioural Biology, Freie Universität, Berlin, Germany
† Department of Life Sciences, Anglia Polytechnic University, Cambridge, UK
‡ Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Correspondence
S. Kiefer, Institute of Biology,
Verhaltensbiologie, Freie Universität, Berlin,
Grunewaldstr. 34, 12165 Berlin, Germany.
E-mail: sarahkiefer7@web.de

Received: January 20, 2006
Initial acceptance: March 15, 2006
Final acceptance: June 20, 2006 (K. Riebel)

doi: 10.1111/j.1439-0310.2006.01283.x

Abstract

Based on the assumptions that birdsong indicates male quality and that quality is related to age, one might expect older birds to signal their age. That is, in addition to actual body condition, at least some song features should vary with age, presumably towards more complexity. We investigated this issue by comparing repertoire sizes of free-ranging common nightingale males in their first breeding season with those of older males. Nightingales are a good model species as they are open-ended learners, where song acquisition is not confined to an early sensitive period of learning. Moreover, nightingales develop an extraordinarily large song-type repertoire (approx. 180 different song types per male), and differences in repertoire size among males are pronounced. We analysed repertoire characteristics of the nocturnal song of nine nightingales in their first breeding season and compared them with the songs of nine older males. The repertoire size of older males was on average 53% larger than that of yearlings. When analysing two song categories of nightingales, whistle and non-whistle songs separately, we found similar results. Our findings show marked differences in repertoire size between age categories, suggesting that this song feature may reflect a male's age. We discuss those mechanisms that may constrain the development of larger repertoires in first-year males. Whether repertoire sizes are crucial for female mate choice or in vocal interactions among conspecific males remains open to further investigations.

Introduction

Many elaborate male characteristics have evolved because of sexual selection (Andersson 1994). The underlying idea is that those elaborate signals are costly and can therefore be only or better performed by higher-quality males. This can in turn be used by females to assess male quality. For many species, it has been shown that older males are more attractive to females (review in Brooks & Kemp 2001). Such preferences might be explained by various factors; e.g. older males are better at parental care (Forslund & Pärt 1995), possess better territories (Catchpole 1986), are less infected with parasites and/or are more immune against pathogens (Saino et al. 2003; Garamszegi et al. 2005). For several bird species, it has been shown that the age of an individual is indeed positively related to its quality in terms of survival and reproduction (review in Martin 1995). The song of many songbird species provides a well-studied example of an elaborate male trait underlying sexual selection and which is often age-dependent.

A study of age-related differences of song characteristics in European starlings *Sturnus vulgaris* revealed that repertoire size increased with age (Mountjoy & Lemon 1995). The same holds true for yellow warblers (*Chloropeta natalensis*, Cosens & Sealy 1986) and for sedge warblers (*Acrocephalus schoenobaenus*, Birkhead et al. 1997). Inconsistent results were found for two populations of great reed warblers (*Acrocephalus arundinaceus*, Catchpole 1986; Hasselquist et al. 1996, discussed in Forstmeier et al. 2006). For other species such as great tits (*Parus major*, McGregor et al. 1981), the correlation between repertoire size and age was not that obvious. Studies considering only adult birds (2 yr and older) conducted on pied flycatchers (*Ficedula hypoleuca*, Espmark & Lampe 1993), song sparrows (*Melospiza melodia*, Searcy et al. 1985, Nordby et al. 2002), and willow warblers (*Phylloscopus trochilus*, Gil et al. 2001) have shown that only some individuals changed certain song characteristics between years. Overall differences between individuals of these species were larger than differences within individuals recorded in successive years. The same result was found in a study of common nightingales (*Luscinia megarhynchos*, referred to as 'nightingale', hereafter; Kipper et al. 2004). The situation is different, however, when one compares song characteristics of birds in their first breeding season (referred to as '1-yr-old', hereafter) with those of older birds. Several species exhibit differences in repertoire size and repertoire composition between these two age classes (brown-headed cowbirds *Molothrus ater artemisia*, O'Loghlen & Rothstein 1993; American redstarts *Setophaga ruticilla*, Lemon et al. 1994; willow warblers, Gil et al. 2001).

Cucco & Malacarne (2000) argued that repertoire increases between the first and following years might be seen as a case of 'delayed maturation', in which all songs are learned during a memorization phase early in life, but only a sub-sample is performed in the first breeding season. Motor constraints or avoidance of specific song types might account for that. Alternatively, males might acquire only a subset of their vocal repertoires in the early sensitive phase and later acquire additional songs that are typically sung on their breeding grounds in a second sensitive phase (e.g. Lemon et al. 1994; Gil et al. 2001). From a functional point of view, such age indicators might be used by conspecific males and females to gain information about the quality of that male. Therefore, songs carry information about the quality of a male, such as its age or actual status, e.g. nutritional or parasitic infection (review in Searcy & Yasukawa 1996). Assuming that repertoire changes occur between breeding seasons but not within them, repertoire size could indicate a male's age. The actual status might rather be reflected by song characteristics such as loudness (Brumm & Todt 2004), singing rates (Garamszegi et al. 2004) or song duration (Lamprechts & Dhondt 1987).

In this study, we compared repertoire characteristics between 1-yr-old and older nightingales. The males of this species possess extraordinarily large song-type repertoires composed of several hundred songs (Hultsch & Todt 1981). A recent longitudinal field study on adult males (age ≥ 2 yr) revealed neither systematic changes of song characteristics with increasing age nor an overall increase in the song repertoire size of males (Kipper et al. 2004). These results were somewhat surprising given that it is known from hand-reared birds that nightingales are capable of learning new song types in their first breeding season (Todt & Geberzahn 2003) and possess 'silent song types'. This term refers to the song types that are memorized during the early sensitive period but are performed only in the second breeding season, possibly triggered by external stimulation such as vocal interactions with conspecifics (Geberzahn et al. 2002; Geberzahn & Hultsch 2003). Thus, if laboratory findings on the song learning of the species are also significant in the field, the critical groups for comparison of song characteristics should be 1-yr-old males and older males. In analysing the singing of these age groups, we applied a cross-sectional approach (for discussion, see Gil et al. 2001; Forstmeier et al. 2006). It is important to note that such an approach does not allow one to discriminate whether a detected difference between age groups is due to continued learning after the first year or reflects a correlation between first-year song characteristics and survival rate. Although one should not easily dismiss the latter possibility, most studies to date showed evidence for the first case (e.g. Eens et al. 1991; Mountjoy & Lemon 1995; Galeotti et al. 2001; Gil et al. 2001; Garamszegi et al. 2005; Forstmeier et al. 2006), but this is not always the case (Gil et al. 2001).

We determined differences in song characteristics such as repertoire size as well as numbers and proportions of whistle and non-whistle songs in the repertoires and the actual song. Whistle songs are a song category that is acoustically distinct and seems to be related to a specific signal value at least in male–male interactions (Naguib et al. 2002). Furthermore, whistle songs are presumably produced in the context of mate attraction (Hultsch 1980; Kunc et al. 2005). Given the evidence for mechanisms of repertoire changes in nightingales, we expected to find differences between the repertoire characteristics of 1-yr-old and older birds. More precisely, we expected larger total repertoire sizes and whistle-song repertoire sizes in older birds when compared with 1-yr-old birds.

Methods

Data Recordings and Subjects

We recorded nocturnal singing bouts (at least 45 min) of nine 1-year-old and nine older nightingales between 24 Apr. and 21 May of the years 2001 ($n_{\text{one year old}} = 1$; $n_{\text{older}} = 1$), 2002 ($n_{\text{one year old}} = 2$; $n_{\text{older}} = 2$), and 2003 ($n_{\text{one year old}} = 6$; $n_{\text{older}} = 6$). For each of the years, recording dates of both age groups were evenly distributed over the respective season and recording date was not correlated to any of our song measures (Spearman's rank correlations, all $n = 18$, all $r < 0.16$, all $p > 0.12$). We assume that, concerning our song measures, there are no potential differences between years. We included all obtained recordings of 1-yr-old nightingales in the analysis and included the same number of randomly chosen recordings of older nightingales to avoid analysing the same bird twice. Our study was conducted in Treptower Park, a municipal park in the city of Berlin, Germany, which covers an area of approx. 0.9 km^2 and is composed of different habitats including dense bushes, clusters of broad-leafed trees, regularly cut grasslands, ponds, and rivers. (For details on the study site, see Kipper et al. 2004.)

For recordings we used Sennheiser ME 80/K3U or ME66/K6 directional microphones (Sennheiser, Wedemark, Germany) with windshields connected to a Sony TCD 5 tape recorder or a Sony WMD 6 walkman (Sony, Köln, Germany). The pairing status of males was not directly monitored, but by recording exclusively nocturnal singing, the males in the sample can be assumed to be of comparable breeding status. In nightingales, nocturnal singing indicates that the singing male is either still unpaired or at the very early stages of breeding at most (Amrhein et al. 2002).

The age of the 1-yr-old nightingales was determined on the basis of morphological features. Birds in their first breeding season usually have characteristic pale tips on their greater secondary coverts and tertials (Glutz von Blotzheim 1988; Svensson 1992). With very few exceptions (in our study only one bird), this age assignment is very reliable. Older nightingales were identified as being at least 2 yr old by having been colour-ringed as adults in previous years. We started to colour-ring birds in 2001 and continued in consecutive years. We captured males with mist nets and song playback after they had been observed for at least 3 d after arrival in the park. Ringing was done with the permission of the Senatsverwaltung für Stadtentwicklung und Umweltschutz and on behalf of the Vogelwarte Radolfzell (Beringungszentrale an der Max-Planck-Forschungsstelle für Ornithologie). No bird deserted its territory after being captured.

Data Acquisition and Analysis

Although we analysed song bouts of different length for the birds, for all analyses presented here we used sequences of 423 consecutive songs (which was the number of successive songs in the shortest sequence recorded). This corresponded to a singing bout of approx. 45 min. In order to determine the repertoire size for each bird, we sampled and analysed continuous singing bouts with a sampling rate of 22 050 Hz and at 16 bit, printed sonagrams (Avisoft SASLab Pro, version 4.23e, R. Specht, Berlin, Germany), and visually compared the songs. We either assigned a given song to a song type already performed or labelled it as a 'new' song type applying the criteria suggested in Hultsch & Todt (1981) and described in detail in Kipper et al. (2004). Nightingales copy songs very precisely and therefore it is possible to assign songs to song types in almost all cases. Nevertheless, to exclude subjectivity in the classification of song types, observers were not aware of the age of the analysed birds.

In addition, we identified the proportion of whistle songs in each song sequence and determined the whistle song repertoire. Differing from other song types that typically consist of several unrepeated frequency modulated elements, whistle songs begin with a homotype series of whistles which may or may not be frequency-modulated (Hultsch & Todt 1996).

For statistical comparisons between the two age classes, we calculated exact (Mundry & Fischer 1998) two-tailed Mann–Whitney U-tests using SPSS 12.0.1. Sample sizes in these tests were always nine 1-yr-old and nine older males.

For one bird (which was not included in the cross-sectional analysis) we were able to obtain recordings from its first and second breeding season. Comparing the repertoire characteristics of this bird longitudinally should allow us to further evaluate the findings of our cross-sectional comparisons. We determined the repertoire sizes for both years, compared the repertoire composition and determined the proportion of whistle songs in the repertoire.

Results

The repertoire size of older males was on average 53% larger than that of 1-yr-old birds (Mann-Whitney U-test: U = 4, p = 0.0005; Fig. 1). When analysing repertoire sizes for whistle- and non-whistle-song types separately, we found that both were significantly larger in older birds (whistle song repertoire size: increase by 30%, U = 13.5, p = 0.015; non-whistle song repertoire size: increase by 57%, U = 3, p = 0.0002; Fig. 2a). Accordingly, we did not find that repertoire increase was due to a disproportionate enlargement of one of the two song categories, as the proportions of whistle songs to non-whistle songs in the repertoire did not significantly differ between the two age groups (U = 22, p = 0.11; Fig. 2b). Finally, yearling males did not differ from older males in how often they produced whistle songs, regardless of type. That is, there was no significant difference between the two age groups with regard to the percentage of whistle songs in the analysed song bout (U = 28, p = 0.286; Fig. 2c).

To substantiate the findings on differences in repertoire characteristics of 1-yr-old and older birds, we did a longitudinal comparison of one bird's song characteristics in its first and second breeding season. The repertoire size of this bird increased by 42% from 114 song types (first breeding season) to 162 songs (second breeding season). Thereby, the bird partially reorganized its repertoire: 55 song types were added in the second breeding season, but some song types (11) were also only performed in the first season. The whistle song repertoire increased by 20% from 20 to 24 different whistle song types. Taken together, the results of this comparison confirmed our findings from the cross-sectional analyses.

Discussion

Our analysis revealed that repertoire size as well as whistle and non-whistle song repertoire sizes were smaller in 1-yr-old than in older nightingales. In fact, the repertoire of older birds was on average 53% larger than that of 1-yr-old males, with almost all 1-yr-old birds having repertoire sizes smaller than those of older males. A longitudinal comparison of one bird supported these findings. Repertoire sizes of older nightingales were well in line with those found in previous studies (Todt 1981; Kipper et al. 2004). Our findings on repertoire differences between the first and second breeding season affirmed our hypothesis that at least some song characteristics should vary with male age and might thus co-vary with male quality. Furthermore, the repertoire increase is consistent with findings on hand-reared nightingales in the laboratory (e.g. Geberzahn & Hultsch 2003) and is in line with results of studies of other bird species such as brown-headed cowbirds (O'Loghlen & Rothstein 1993), willow warblers (Gil et al. 2001),

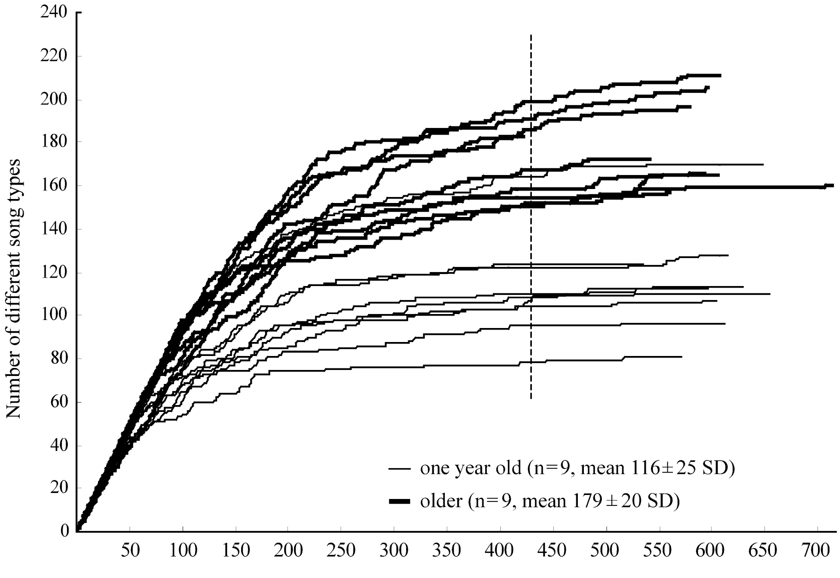

Fig. 1: Repertoire saturation for 1-yr-old and older nightingales. Depicted are the cumulative number of song types against the number of songs analysed. The dashed line indicates the reference point for the comparison of repertoire sizes

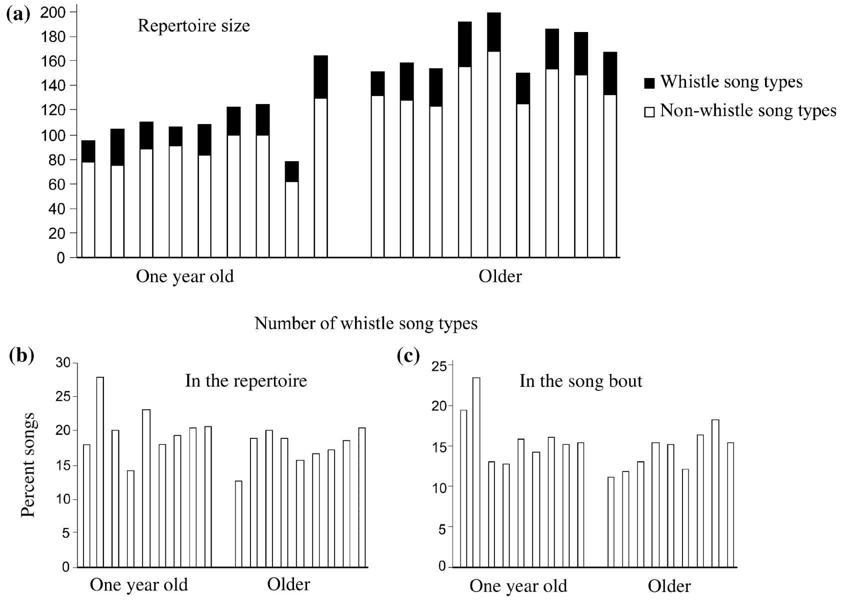

Fig. 2: Repertoire characteristics of nine 1-yr-old and nine older nightingales. Indicated are numbers of non-whistle and whistle songs (a) in individual repertoires as well as the percentage of whistle songs in repertoires (b) and in the analysed song bouts (c). Each bar shows values for one subject. The order of subjects is the same in all graphs. All values refer to a sequence of 423 songs. Note that scales of y-axes differ between graphs

yellow warblers (Cosens & Sealy 1986) and sedge warblers (Birkhead et al. 1997). Our study expands these findings on repertoire increases to include a species with extremely large song-type repertoires.

Together with the finding that older nightingales do not generally increase their repertoire size between successive breeding seasons (Kipper et al. 2004), our results suggest that a dramatic increase in repertoire size occurs between the first and the second breeding season, whereas afterwards the repertoire size of each individual remains at a particular, though individually different level (Kipper et al. 2004). To what degree the repertoire size of first-year males and the same males being fully adult are interrelated and, hence, to what degree the repertoire size of an individual nightingale is already determined early in life, warrant further research.

Our results raise the question of how enlarged repertoires are developed. Three possibilities could be considered: (1) birds may indeed learn new song types during their first breeding season (as was shown by Todt & Geberzahn 2003 for hand-reared nightingales) or after fall migration; (2) recombination of learned song material may take place (Hughes et al. 2002) or (3) 'silent song types' are possibly triggered by external stimulation such as vocal interactions with conspecifics (Geberzahn et al. 2002; Geberzahn & Hultsch 2003). Our mainly cross-sectional study includes the problem that differences in repertoire sizes can be explained not only by learning but also by quality-dependent survival. Although one should not easily dismiss the latter possibility, most studies showed evidence for the first case (e.g. Eens et al. 1991; Mountjoy & Lemon 1995; Galeotti et al. 2001; Gil et al. 2001; Garamszegi et al. 2005; Forstmeier et al. 2006).

In functional terms, such repertoire increase seems to represent a case of delayed maturation as proposed by Gil et al. (2001). In that study, it was assumed that delayed maturation in characteristics such as repertoire size is due to costs, such as neural, social or immunity costs. Our findings raise the question of whether nightingales are possibly not true open-ended learners, but have two sensitive phases: one as fledglings and a second to adjust their repertoire specifically to the songs sung at their breeding grounds. Such separated sensitive phases have been assumed for other species as well (e.g. Lemon et al. 1994; Gil et al. 2001). Accordingly, differences in song characteristics would be a reliable indicator of a bird's age and related quality (Martin 1995). Among the many hypotheses on factors promoting repertoire size (review in Catchpole & Slater 1995; Slater 2003), inter-sexual selection plays a crucial role. Female sedge warblers, for example, prefer to mate with males with larger repertoires (e.g. Catchpole et al. 1984). A study by Kipper et al. (2005) found that repertoire size in nightingales is indeed correlated to body measures and arrival date, properties that might be correlated with male quality. It remains open as to whether or how female nightingales evaluate male song. Even if repertoire size is not the feature directly selected for, it might affect the song characteristics that are crucial for female mate choice (for number of songs that are harder to perform, song versatility, or frequency of song type matching, see below).

Intra-sexual selection may as well play a crucial role in the evolution of larger repertoires (Hiebert et al. 1989; Forstmeier & Leisler 2004) by, for example, affecting the outcome of territorial interactions between males. It has been shown that it is advantageous for males to have a large repertoire when engaging in 'song-type matching' (review in Todt & Naguib 2000). Furthermore, it is conceivable that female choice is based on such male–male interactions (e.g. Otter et al. 1999). Thus females could indirectly prefer larger repertoires (e.g. by evaluating the frequency with which males song type match). Considering the category of whistle songs, we found neither age-dependent differences in the proportion of whistle songs in the repertoire, nor age-dependent differences in the proportion of whistle songs in the actual song performance. Studies on the role of whistle songs suggest that they might be important in interactions between males (Naguib et al. 2002) as well as in attracting females (Hultsch 1980; Kunc et al. 2005). Referring to the latter function, we would not have been surprised to find differences between the two age classes with regard to the proportion of whistle songs in repertoires or song sequences. As our findings did not reveal such differences, we conclude that from the perspective of song development and potential production constraints, whistle songs are no special song category in 1-yr-old males.

To summarize, our finding that first-year and older nightingales differ considerably in repertoire size, invites to address a number of questions. First of all, it remains open as to whether these obvious differences are used by nightingales as a reliable indicator of a singer's age (and potentially its quality) and what exact role this plays in interactions between males and for mate choice by females. Secondly, it raises the question of whether first-year males enlarge their repertoire by activating 'silent songs' or by acquiring new songs. Assuming that repertoire size is not a crucial feature per se, future studies should address whether 1-yr-old and older males differ not only in repertoire size but also in the particular composition of their repertoires. For example, it seems conceivable that certain song types are more complicated to acquire and/or to sing and, as a result, are particularly uncommon in first-year males. A particularly interesting question is how the finding of our study relates to that of Kipper et al. (2004) who found that repertoire size and composition do not change once a nightingale is fully mature (i.e. at least 2 yr of age). In fact, these two findings combined raise the question of whether the repertoire size of males in their first year is (positively) correlated to that of the same males later in life. Such a correlation would indicate that early experience (i.e. parental care) and/or genetic quality may be expressed only after 2 yr of development – a considerable age for a small bird with such a short lifespan.

Acknowledgements

We thank Christoph Teufel, Christoph Lange, Philipp Sprau, Martina Koch, Henrik Brumm and Petra Selchow for their kind help with data collection. We are also thankful to the Vogelwarte Radolfzell and the Senatsverwaltung für Stadtentwicklung und Umweltschutz for the permission to colour-ring and observe the nightingales, and their friendly support for this ongoing project.

Literature Cited

Amrhein, V., Korner, P. & Naguib, M. 2002: Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. Anim. Behav. **64**, 939—944.

Andersson, M. 1994: Sexual Selection. Princeton Univ. Press, Princeton, NJ.

Birkhead, T. R., Buchanan, K. L., Devoogd, T. J., Pellatt, E. J., Székely, T. & Catchpole, C. K. 1997: Song, sperm quality and testes asymmetry in the sedge warbler. Anim. Behav. **53**, 965—971.

Brooks, R. & Kemp, D. J. 2001: Can older males deliver good genes? Trends Ecol. Evol. **16**, 308—313.

Brumm, H. & Todt, D. 2004: Male-male vocal interactions and the adjustment of song amplitude in a territorial bird. Anim. Behav. **67**, 281—286.

Catchpole, C. K. 1986: Song repertoires and reproductive success in the great reed warbler *Acrocephalus arundinaceus*. Behav. Ecol. Sociobiol. **19**, 439—445.

Catchpole, C. K. & Slater, P. J. B. 1995: Bird Song – Biological Themes and Variations. Cambridge Univ. Press, London.

Catchpole, C. K., Dittami, J. & Leisler, B. 1984: Differential responses to male song repertoires in female songbirds implanted with oestradiol. Nature **312**, 563—564.

Cosens, S. E. & Sealy, S. G. 1986: Age-related variation in song repertoire size and repertoire sharing of yellow warblers. Can. J. Zool. **64**, 1926—1929.

Cucco, M. & Malacarne, G. 2000: Delayed maturation in passerine birds: an examination of plumage effects and some indications of a related effect in song. Ethol. Ecol. Evol. **12**, 291—308.

Eens, M., Pinxten, R. & Verheyen, R. F. 1991: No overlap in song repertoire size between yearling and older starlings *Sturnus vulgaris*. Ibis **134**, 72—76.

Espmark, Y. O. & Lampe, H. M. 1993: Variations in the song of the pied flycatcher within and between breeding seasons. Bioacoustics **5**, 33—65.

Forslund, P. & Pärt, T. 1995: Age and reproduction in birds – hypotheses and tests. Trends Ecol. Evol. **10**, 374—378.

Forstmeier, W. & Leisler, B. 2004: Repertoire size, sexual selection, and offspring viability in the great reed warbler: changing patterns in space and time. Behav. Ecol. **15**, 555—563.

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**, 634—643.

Galeotti, P., Saino, N., Perani, E., Sacchi, R. & Møller, A. P. 2001: Age-related song variation in male barn swallows. It. J. Zool. **68**, 305—310.

Garamszegi, L. Z., Møller, A. P., Török, J., Michl, G., Péczely, P. & Richard, M. 2004: Immune challenge mediates vocal communication in a passerine bird: an experiment. Behav. Ecol. **15**, 148—157.

Garamszegi, L. Z., Heylen, D., Møller, A. P., Eens, M. & de Lope, F. 2005: Age-dependent health status and song characteristics in the barn swallow. Behav. Ecol. **16**, 580—591.

Geberzahn, N. & Hultsch, H. 2003: Long-time storage of song types in birds: evidence from interactive playbacks. Proc. R. Soc. Lond. B **270**, 1085—1090.

Geberzahn, N., Hultsch, H. & Todt, D. 2002: Latent song type memories are accessible through auditory stimulation in a hand-reared songbird. Anim. Behav. **64**, 783—790.

Gil, D., Cobb, J. L. S. & Slater, P. J. B. 2001: Song characteristics are age dependent in the willow warbler, *Phylloscopus trochilus*. Anim. Behav. **62**, 689—695.

Glutz von Blotzheim, U. N. 1988: Handbuch der Vögel Mitteleuropas. Band 11, AULA-Verlag, Wiesbaden.

Hasselquist, D., Bensch, S. & von Schantz, T. 1996: Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature **381**, 229—232.

Hiebert, S. M., Stoddard, P. K. & Arcese, P. 1989: Repertoire size, territory acquisition and reproductive success in the song sparrow. Anim. Behav. **37**, 266—273.

Hughes, M., Hultsch, H. & Todt, D. 2002: Imitation and invention in song learning in nightingales (*Luscinia megarhynchos* B., Turdiae). Ethology **108**, 97—113.

Hultsch, H. 1980: Beziehungen zwischen Struktur, zeitlicher Variabilität und sozialem Einsatz im Gesang der Nachtigall (*Luscinia megarhynchos*). Dissertation, Freie Universität Berlin, Berlin.

Hultsch, H. & Todt, D. 1981: Repertoire sharing and song post distance in nightingales. Behav. Ecol. Sociobiol. **8**, 183—188.

Hultsch, H. & Todt, D. 1996: Rules of parameter variation in homotype series of birdsong can indicate a 'sollwert' significance. Behav. Proc. **38**, 175—182.

Kipper, S., Mundry, R., Hultsch, H. & Todt, D. 2004: Long-term persistence of song performance rules in nightingales (*Luscinia megarhynchos*): a longitudinal field study on repertoire size and composition. Behaviour **141**, 371—390.

Kipper, S., Mundry, R., Sommer, C., Hultsch, H. & Todt, D. 2005: Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. Anim. Behav. **71**, 211—217.

Kunc, H. P., Amrhein, V. & Naguib, M. 2005: Acoustic features of song categories and their possible implications for communication in the common nightingale (*Luscinia megarhynchos*). Behaviour **142**, 1083—1097.

Lamprechts, M. & Dhondt, A. A. 1987: Differences in singing performance between male great tits. Ardea **75**, 43—52.

Lemon, R., Perreault, S. & Weary, D. 1994: Dual strategies of song development in American redstarts *Setophaga ruticilla*. Anim. Behav. **47**, 317—329.

Martin, K. 1995: Patterns and mechanisms for age-dependent reproduction and survival in birds. Am. Zool. **35**, 340—348.

McGregor, P. K., Krebs, J. R. & Perrins, C. M. 1981: Song repertoires and lifetime reproductive success in the great tit (*Parus major*). Am. Nat. **118**, 149—159.

Mountjoy, D. J. & Lemon, R. E. 1995: Extended song learning in wild European Starlings. Anim. Behav. **49**, 357—366.

Mundry, R. & Fischer, J. 1998: Use of statistical programs for nonparametric tests of small samples often leads to incorrect p-values: examples from Animal Behaviour. Anim. Behav. **56**, 256—259.

Naguib, M., Mundry, R., Hultsch, H. & Todt, D. 2002: Responses to playback of whistle songs and normal songs in male nightingales: effects of song category, whistle pitch, and distance. Behav. Ecol. Sociobiol. **52**, 274—285.

Nordby, J. C., Campbell, S. E. & Beecher, M. D. 2002: Adult song sparrows do not alter their song repertoires. Ethology **108**, 39—50.

O'Loghlen, A. & Rothstein, S. I. 1993: An extreme example of delayed vocal development: song learning in a population of wild brown-headed cowbirds. Anim. Behav. **46**, 293—304.

Otter, K., McGregor, P. K., Terry, A. M. R., Burford, F. R. L., Peake, T. M. & Dabelsteen, T. 1999: Do female graet tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. Proc. R. Soc. Lond. B **266**, 1305—1309.

Saino, N., Galeotti, P, Sacchi, R. & Møller, A. P. 2003: Humoral immune response in relation to senescence, sex, and sexual ornamentation in the barn swallow (*Hirundo rustica*). J. Evol. Biol. **16**, 1127—1134.

Searcy, W. A. & Yasukawa, K. 1996: Song and female choice. In: Ecology and Evolution of Acoustic Communication in Birds (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, NY; London, pp. 454—473.

Searcy, W. A., McArthur, P. D. & Yasukawa, K. 1985: Song repertoire size and male quality in song sparrows. Condor **87**, 222—228.

Slater, P. J. B. 2003: Fifty years of bird song research: a case study in animal behaviour. Anim. Behav. **65**, 633—639.

Svensson, L. 1992: Identification Guide to European Passerines. British Trust for Ornithology, Thetford.

Todt, D. 1981: On functions of vocal matching: effect of counter-replies on song post choice and singing. Zeitschrift für Tierpsychologie **57**, 73—93.

Todt, D. & Geberzahn, N. 2003: Age-dependent effects of song exposure: song crystallisation sets a boundary between fast and delayed vocal imitation. Anim. Behav. **65**, 971—979.

Todt, D. & Naguib, M. 2000: Vocal interactions in birds: The use of song as a model in communication. Adv. Study Behav. **29**, 247—296.