# Age-Dependent Expression of Song in the Collared Flycatcher, *Ficedula albicollis*

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**Abstract**

Theory suggests that male ornaments should be reliable signals of age, with more elaborated ornaments reflecting superior quality in terms of experience and/or viability. Bird song is immensely involved in sexual selection, thus not-surprisingly, it usually shows age-dependent variation. Although the collared flycatcher *Ficedula albicollis* has been intensively studied for its sexual traits, and female preference for male age is expected to be strong, there is no quantitative information on age-dependent expression of song in this species. Here, we fill this gap and, based on phenotypic correlations, we report the relationship between age and several song features. Repertoire size was consistently smaller in yearlings than in older males, but it also tended to increase after the second year of breeding. In a meta-analysis of effect sizes using data from the literature, we found that the strength of the relationship between age and repertoire size in the collared flycatcher is similar to patterns observed in other passerines. Song rate was inversely related to age, as yearlings sang at higher rates than older males. Generally, effect sizes for the relationship between age and other song traits were of medium level on average, and had broad confidence intervals. Song traits covaried with survival in a direction suggesting that differences in song between age categories are unlikely to result from phenotype dependent survival. Our results generally support the hypothesis that song holds the potential to function as a reliable indicator of male age in the collared flycatcher. However, it seems that not all song traits are unambiguously more expressed in older males than in yearlings.

## Introduction

Age has been hypothesized to play a role in sexual selection, as male ornaments are often more developed in older individuals than in yearlings (Trivers 1972; Manning 1985; Andersson 1994). Age-dependent elaboration of sexual signals may be explained in two ways. First, the ornament may be designed to signal male age per se, as male quality may reflect viability. Secondly, the ornament may reflect male condition that improves with age through experience. Therefore, if trait expression reliably signals male age, choosy females may benefit from pairing with older individuals as a result of preferring extravagant sexual characters. Females mating with such males may obtain either direct fitness benefits, if older males have territories of high quality (Alatalo et al. 1986a), provide superior parental care through improved foraging or defense against predators (Yasukawa 1981; Alatalo et al. 1986b; Marchetti & Price 1989) or absence of pathogens (Saino et al. 2003), or they may obtain genetic benefits for the offsprings, if viability is heritable (Trivers 1972).

Sexual selection has been assumed to maintain extravagant song displays in birds, because bird song

is used in both male–male competition and female choice (Searcy & Yasukawa 1996; Searcy & Nowicki 2000). In fact, bird song is a typical trait that is known to vary consistently between age classes. This may occur because (i) the song changes during life (within-individual changes), or (ii) there is differential survival with respect to song (phenotype-dependent survival). In many oscine species, repertoire size is different between different age categories (Nottebohm & Nottebohm 1978; Cosens & Sealy 1986; Eens et al. 1992a,b; Espmark & Lampe 1993; Mountjoy & Lemon 1995; Hasselquist et al. 1996b; Birkhead et al. 1997; Galeotti et al. 2001; Gil et al. 2001; Garamszegi et al. 2005), although this is not always the case (McGregor et al. 1981; Searcy et al. 1985; Catchpole 1986). Song learning is ubiquitous in oscine passerines, and the continuous acquisition of new elements may depend on learning processes (Kroodsma 1982). Alternatively, birds might acquire their repertoires during their sensitive phase in early ontogeny, which they do not perform entirely in their first breeding season ('silent song types'; Geberzahn et al. 2002). Therefore the link between age and repertoire size may be largely due to processes associated with within-individual changes. Accordingly, longitudinal analyses of the same individuals revealed that repertoire size increases from young to older birds (Eens et al. 1992a,b; Galeotti et al. 2001; Gil et al. 2001). Studies that tested for similar relationships between other song attributes (e.g. song performance or song structure) and male age have shown inconsistent results (Galeotti et al. 2001; Gil et al. 2001).

On the other hand, little is known about the relationship between survival and song, although theories predict such a relationship. In general, the relationship between sexual traits and survival should strike an optimal balance between the costs and benefits of sexual advertisement that depend on life-history trade-offs and mating skew (Brooks & Kemp 2001; Kokko et al. 2002). Survival and trait expression are classically believed to be mediated by male quality, and females preferring elaborate signals will more likely mate with individuals carrying good genes for survival (Trivers 1972; Andersson 1994). Hence, a positive relationship between song and survival is well expected. However, favored by strong female preference, males may advertise their quality so intensively that this has deteriorating consequences for survival (Kokko et al. 2002), which in fact should result in a negative relationship between survival and the elaboration of songs. The general pattern indicates that the expression of sexual traits

is usually positively associated with male viability (Jennions et al. 2001). Song length may predict viability in the great tit, *Parus major*, as it was positively related to survival (Lambrechts & Dhondt 1986). Showing a relationship with survival is important, because it can indicate that song differences across age categories appear due to phenotype-dependent survival (Forstmeier 2002).

Here, we present phenotypic correlations between male age, survival and song traits in a Hungarian population of the collared flycatcher, *Ficedula albicollis*. Previously, we have shown that song may be a reliable signal of male quality as parasitism and metabolic constraints due to stress can affect song characteristics (Garamszegi et al. 2004a; Garamszegi et al. 2006). Male age was not a confounding factor in these specific contexts. The relationship between male age and sexual signals is well established for plumage traits (Gustafsson et al. 1995; Hegyi et al. 2002; Török et al. 2003; Wiley et al. 2005). However, the age-dependence of song in this intensively studied species remains unknown, although it would be important in the broader context of sexual selection. To fill this gap, we assess the magnitude of age-effects on various song traits. A relationship between age and song may result from within-individual changes (e.g. due to learning or other aging effects) and/or from between-individual changes (e.g. due to phenotype-dependent survival). Hence, we made an effort to disentangle between these two mechanisms by estimating the association between song and survival. If the age-dependent expression of song is due to within-individual changes, we predicted that age-related song traits vary independently of survival. In contrast, if phenotype-dependent survival shapes age differences in song, we predicted that relationships between survival and features of song will be consistent in direction and strength with relationships between age and song.

## Methods

### General Methods

The collared flycatcher is a small insectivorous, socially monogamous hole-nesting passerine (Cramp & Perrins 1994). After arriving at the breeding sites, males immediately occupy nest boxes or natural cavities, and establish territories where they start singing and displaying. Females visit several males, and may prefer males with songs of superior quality, but song may also be important in a male–male context (Garamszegi et al. 2004a). We established breeding

plots at Pilis Field Station near Budapest (47°43′N, 19°01′E), Hungary in 1981 for a long-term study of the species (see Török & Tóth 1988). Fieldwork for the current study was carried out during 2004–2005, when we recorded the song of unmanipulated and unpaired males as described below.

## Song Recordings and Sonagraphic Analyses

Altogether, we recorded unpaired males by using a Sony (Sony Electronics Inc., NY, USA) TCD-D8 DAT tape recorder (in 2004) or Sony Minidisc Recorder MZ-N1 (in 2005) and a MD 21 U microphone during the most active morning singing period (usually between 05.00 and 10.00). We recorded each male for at least 10 min to obtain a sufficient number of songs with minimal background noise. Recordings were made only in relatively good weather conditions. We obtained good quality recordings for 37 males, each recorded only on a given day, during an observation no longer than an hour.

The song of the collared flycatcher consists of 2- to 3-s-long strophes, which are uninterrupted series of acoustic elements so-called figures with pauses no longer than 1 s (Fig. 1). Songs were analyzed after the field season by a single observer (LZG) using the computer program 'Avisoft-SASLab Pro' (Specht

1999) blindly with respect to age. The best resolution was achieved in the 0–20 kHz frequency range, using Hamming evaluation window, with FTT-Length of 256 points, band width of 254 Hz, frequency resolution of 195 Hz, and time resolution of 5.12 ms. We estimated song rate as the number of strophes/min based on the available recordings. We selected 20 consecutive strophes of good record quality that allowed song analyses without subsequent filtering. We measured the following variables for each strophe: strophe length in seconds, no. of figures, versatility (no. of unique figures within strophe), complexity (no. of unique figures/no. of figures within strophe), and tempo (no. of figures/s). Given the repeatability of these song traits within individuals (see Garamszegi et al. 2004a; Garamszegi 2006 for details), we averaged these variables for each male.

Total figure repertoire size was estimated by the inspection of the entire sample of 20 strophes. First, we compiled a collection of printed spectrograms, and visually compared each figure. We either assigned a given figure to a given type that had already been detected, or labeled it as a new type. Finally, we counted the number of figure types we found over the 20 spectrograms to yield the male's repertoire size. Previously, we demonstrated that the
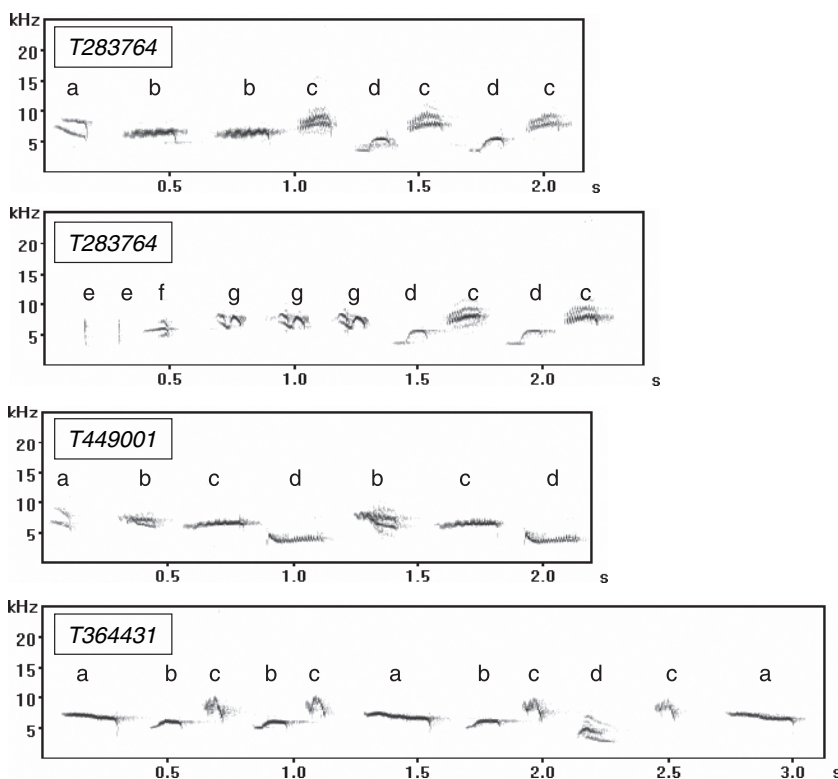


Fig. 1: Spectrographic representation of four strophes from three collared flycatcher males (ring numbers are given in the upper left corners). Elements within strophes are called figures, which are labeled with letters. Each letter type corresponds to a figure type from the given male's repertoire. Note that the alphabet is comparable between different strophes of the same male, but not between different males

cumulative plot of figures in relation to the number of strophes analyzed levels off after 15 strophes, so our repertoire size estimate based on a sample of 20 strophes should be close to the true repertoire size (Garamszegi et al. 2002). In addition, we have shown that our estimation of repertoire size was biologically meaningful, as it could be assessed on a repeatable way even if songs were sampled on different days, and it was positively related to testosterone levels (Garamszegi et al. 2004a). Although in previous works, our general practice was to use capture-recapture approach to estimate repertoire size (Garamszegi et al. 2004a; Garamszegi 2006), in this study we relied on simple counts of unique figures in 20 strophes in order to obtain data suited for a comparison with other studies.

## Age and Survival

After making recordings in the field, males were trapped and measured for standard morphological traits. Based on the typical sub-adult plumage coloration of yearling males (brown remiges), we classified individuals as yearlings or older birds (Svensson 1984). Relying on our standard banding protocol we apply in each breeding season (Garamszegi et al. 2004b; see Hegyi et al. 2002; Hegyi et al. 2002, 2006b; Török et al. 2003, 2004), and using information on our estimates of age from previous years, we could also assess the exact age of recaptured birds from our long-term record. Therefore, we used a binary variable to reflect differences between year-

lings (age 1) and older birds (older than age 1), and also a continuous variable to focus on age differences in older age categories (from age 2 until age 7). With these two estimates of age, we could assess whether any age-dependent variation occurs only between yearlings and older males, or also with exact age of older males. This separation is important because it enabled us to capture aging related effects that occurred in different stages of life.

Male survival was estimated based on recapture data. Those males that were re-captured in a subsequent breeding season were considered as surviving males, while individuals not seen in the future were considered non-surviving. Survival was not confounded by age, as yearlings were equally likely to survive as older birds ($\chi^2 = 0.013$, p = 0.908). For each male, only data from a single year was used, thus each measurement represents an independent observation (we obtained song recordings in both years for one male, for which only data from 2004 were used).

## Statistical Approaches

Mean (±SE) values of song traits are given in Table 1. These variables were checked for normality and homoscedasticity, and $\log_{10}$-transformation was applied to repertoire size in order to meet the parametric criteria. There are many significant correlations among song traits (Table 1), which is generally due to the fact that some traits capture similar biologic phenomena. Previously, we reduced the

**Table 1:** Mean (±SE) values of song traits and their pair-wise correlations (Pearson's *r*) together with the associated 95% confidence intervals in the collared flycatcher (n = 37). Repertoire size is given for samples of 20 strophes by using simple syllable count. Song rate is for the whole recording, while versatility, complexity and tempo refer to a single strophe

| | x̃ ± SE | Effect size correlations (95% CI: lower CI/upper CI) | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | RATE | VERS | TEM | LEN | COMP | FIG |
| Repertoire size | 26.9 ± 1.5 | −0.01 | 0.55 | 0.33 | 0.16 | 0.21 | 0.28 |
| REP | | −0.34/0.31 | 0.28/0.74 | 0.01/0.59 | −0.17/0.46 | −0.12/0.50 | −0.05/0.55 |
| Song rate (min⁻¹) | 4.07 ± 0.23 | | 0.02 | −0.29 | 0.11 | 0.15 | 0.00 |
| RATE | | | −0.31/0.34 | −0.56/0.04 | −0.22/0.42 | −0.18/0.46 | −0.33/0.32 |
| Versatility | 6.66 ± 0.22 | | | 0.26 | 0.64 | 0.16 | 0.78 |
| VERS | | | | −0.17/0.46 | 0.40/0.80 | −0.17/0.46 | 0.61/0.88 |
| Tempo (s⁻¹) | 3.63 ± 0.07 | | | | −0.23 | −0.23 | 0.28 |
| TEM | | | | | −0.52/0.10 | −0.51/0.10 | −0.05/0.55 |
| Strophe length (s) | 2.93 ± 0.09 | | | | | −0.36 | 0.82 |
| LEN | | | | | | −0.61/−0.04 | 0.68/0.91 |
| Complexity (%) | 0.65 ± 0.01 | | | | | | −0.39 |
| COMP | | | | | | | −0.64/−0.08 |
| No. figures | 10.4 ± 0.4 | | | | | | |
| FIG | | | | | | | |

The strongest correlations, which probably indicate that the two song variables describe the same phenomena, are highlighted.

number of statistical tests performed with multiple song features by using principal component analysis, which provided us with measures of song structure and complexity that are uncorrelated with each other (Garamszegi et al. 2004a, 2006a). However, in this study, in order to get data comparable to studies on other bird species, we focused on the original song variables that are independent of each other. Therefore, we eliminated those variables that strongly correlated (r > 0.5) with other marker features. Accordingly, we removed the number of figures and strophe versatility because they reflected strophe length and strophe complexity (Table 1).

To test for the relationship between song, age and survival, we applied Student's t-test and Pearson's correlation in a cross-sectional design. To separate effects due to phenotype-dependent survival from effects due to systematic individual change that may both result in apparent differences between age categories, the combination of longitudinal and cross-sectional approaches should be preferred (Gil et al. 2001; Török et al. 2003). However, due to lack of data, we were not able to perform longitudinal analyses of the same individuals over consecutive years to test for consistent individual changes. As an alternative, we directly tested whether survival/mortality differed between males with different song characteristics (Forstmeier 2002). Accordingly, if a song feature differs between age categories because of changes within individuals, one can expect a relationship with age but not with survival. In contrast, if age-differences are due to differences in survival, there should be a relationship with both age and survival, in a consistent direction.

For each relationship, we calculated effect sizes (Cohen's d sensu Cohen 1988), and the associated 95% confidence intervals (CI) from the corresponding statistics. In general, effect size is a standard and comparable estimate of the strength and direction of the investigated relationship, which takes differences in sample size into account (Cohen 1988). As a benchmark for research design, Cohen (1988) suggested 'conventional' values for small, medium, and large effects, as d = 0.20, 0.50, and 0.80, respectively. Although we also report conventional statistical results (Table 2), we preferred focusing on effect sizes (Table 3). We did not use Bonferroni correction on significance levels, because this approach has been criticized in the field of ecology and behavioral ecology for mathematical and logical reasons (Perneger 1998; Moran 2003; Nakagawa 2004; Garamszegi 2006). We used the software Comprehensive Meta Analysis (BioStat 2000, http://www.meta-analysis.com/)

**Table 2:** The relationship between song variables and estimates of age and survival in male collared flycatcher using conventional statistical approaches. The effect size for each relationship is given in Table 3. Age as a binary variable captures differences between yearling and older birds, while age as a continuous variable reflects the exact age of individuals older than one year. When categories are compared, group-specific means (and standard errors in brackets) are given

| | Age$_{binary}$ n$_{Yearlings}$ = 13 n$_{Adults}$ = 24 | Age$_{continuous}$ n = 24 | Survival n$_{Survivors}$ = 14 n$_{Non-suvivors}$ = 23 |
|---|---|---|---|
| Repertoire size | Yearlings: 22.6 (1.5), Adults: 29.2 (2.0); $t_{35}$ = 2.12, p = 0.041 | r = 0.374, p = 0.072 | Survivors: 26.6 (2.9), Non-survivors: 27.0 (1.7); $t_{35}$ = −0.41, p = 0.688 |
| Song rate | Yearlings: 4.83 (0.42), Adults: 3.66 (0.25); $t_{35}$ = −2.56, p = 0.015 | r = −0.146, p = 0.497 | Survivors: 4.17 (0.34), Non-survivors: 4.01 (0.32); $t_{35}$ = 0.33, p = 0.747 |
| Tempo | Yearlings: 3.47 (0.11), Adults: 3.72 (0.09); $t_{35}$ = 1.63, p = 0.111 | r = 0.016, p = 0.941 | Survivors: 3.71 (0.16), Non-survivors: 3.58 (0.06); $t_{35}$ = 0.91, p = 0.372 |
| Strophe length | Yearlings: 2.83 (0.13), Adults: 2.99 (0.13); $t_{35}$ = 0.80, p = 0.431 | r = −0.240, p = 0.260 | Survivors: 3.03 (0.16), Non-survivors: 2.87 (0.12); $t_{35}$ = 0.82, p = 0.416 |
| Complexity | Yearlings: 0.68 (0.02), Adults: 0.63 (0.01); $t_{35}$ = −1.67, p = 0.104 | r = 0.184, p = 0.389 | Survivors: 0.63 (0.02), Non-survivors: 0.66 (0.02); $t_{35}$ = −1.22, p = 0.231 |

**Table 3:** Effect sizes (Cohen's d) and the associated 95% confidence intervals (CI) for the relationship between male age, survival and features of song. Effect size conventions: d = 0.20 small effect, d = 0.50 medium effect, d = 0.80 large effects (Cohen 1988). Signs of effects indicate whether the direction of the relationship showed larger (+) or smaller (−) values in older than in younger males, or in survivors than in non-survivors. Age as a binary variable captures differences between yearling and older birds, while age as a continuous variable reflects the exact age of older (>age 1) individuals

|  | Effect sizes (Cohen's d) (95% CI: lower CI/upper CI) | | |
|---|---|---|---|
|  | Age (binary) (n = 37) | Age (continuous) (n = 24) | Survival (n = 37) |
| Repertoire size | 0.73 (0.03/1.42) | 0.81 (−0.07/1.83) | −0.14 (−0.80/0.53) |
| Song rate | −0.88 (−1.59/−0.18) | −0.29 (−1.21/0.57) | 0.11 (−0.56/0.78) |
| Tempo | 0.56 (−0.12/1.25) | 0.03 (−0.85/0.92) | 0.31 (−0.36/0.98) |
| Strophe length | 0.28 (−0.40/0.95) | −0.49 (−1.45/0.37) | 0.28 (−0.39/0.95) |
| Complexity | −0.58 (−1.26/0.11) | 0.37 (−0.49/1.31) | −0.41 (−1.08/0.26) |

to calculate the effect sizes and the corresponding CIs.

The use of effect sizes was especially useful because it allowed us to compare quantitatively our results with findings on other species. We compared effect size for the relationship between age and repertoire size with literature data by using a meta-analytic approach (see Thompson 2002). First, based on a systematic electronic search using PubMed (http://www.ncbi.nlm.nih.gov/PubMed) and Web of Science (http://isi1.isiknowledge.com), we collected published results of studies investigating the relationship between age and song using cross-sectional approaches. Secondly, test statistics or significance levels were transformed into effect size (Cohen's d), as a common currency (Rosenthal 1991; Cooper & Hedges 1994). We included analyses based on t-test (two-tailed), or other equivalent statistics testing the null hypothesis that yearling males have similar repertoire to older males. The estimated effect sizes were entered in a meta-analysis in which we calculated the overall effect size for the literature data, and compared it with effect size found in this study (see Thompson 2002). Results on other song traits or on differences between age categories were too scarce to permit an informative meta-analytic comparison.

## Results

The relationships between song and age, and between song and survival are given in Tables 2 and 3. Yearlings had smaller repertoires than older males, and this effect was comparable to previously reported differences between these age categories (Fig. 2). We found similar effect sizes when we used the exact age of older males, and thus focused on differences in repertoire size among older males based on a linear approach (Table 3). However, due to the lower sample size, these effects could only be estimated with a broader CI.

Strong effects were found for the relationship between age and song rate, but only when focusing on the differences between yearlings and older males (Table 3). This effect indicated that yearlings sang at higher rates than older males. The effect size for the relationship between binary age and other features of song appeared to be less robust, but notably, medium effects were associated with strophe tempo and complexity (Table 3). In general, the average strength of the relationship between song and age as reflected by the mean of unsigned effect sizes was 0.61 (SE = 0.10). When treating older male age on a continuous scale, effect sizes tended to be different from those based on the binary categorization of yearlings vs. older males (x ± SE of unsigned effect sizes: 0.40 ± 0.13). Arising from the constraints of the study of bird song due to limited sample sizes, we generally could estimate the above effects with broad confidence intervals (Table 3).

If age differences principally arise due to the phenotype-dependent survival, we predicted effect sizes for the relationship between survival and song being similar to effect sizes for the relationship between age and song. However, this was clearly not the case. We found effects that varied inconsistently to age effects on song (Table 3). The inconsistency is the most remarkable with respect to repertoire size and song rate. We detected a relatively strong and positive relationship between repertoire size and age. However, a similar relationship did not emerge for survival, which could be expected if age-dependence of a trait is mediated by phenotype-dependent survival. Song rate was negatively related to age, but it appeared to have no remarkable survival indicator value (Table 3). Generally, the strength of the relationship between song and survival was of weak magnitude (x ± SE of unsigned effect sizes: 0.25 ± 0.06).

## Discussion

In the collared flycatcher, we demonstrated that repertoire size differed strongly between yearlings and older males. A similar tendency was found when we
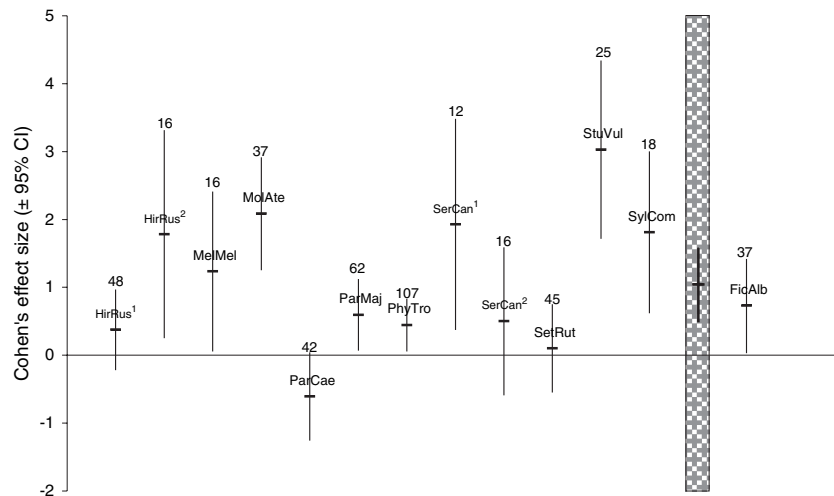
**Fig. 2:** The difference in repertoire size between yearlings and older males in different species as estimated by Cohen's d effect size and the associated 95% confidence intervals (CI). Positive effects indicate the expected trend, in which yearlings have smaller repertoire size than adults. Combined effect size (gray-outlined) was calculated for the literature data by a meta-analytic approach, which is compared with the effect size found (FicAlb) in the current study (see Methods). HirRus[1]: barn swallow, *Hirundo rustica* from Galeotti et al. (2001); HirRus[2]: barn swallow from Garamszegi et al. (2005); MelMel: song sparrow, *Melospiza melodia* from Hiebert et al. (1989); MolAte: brown-headed cowbird, *Molothrus ater* from O'Loghlen & Rothstein (2002); ParCae: blue tit, *Parus caeruleus* from Bijnens (1988); ParMaj: great tit, *Parus major* form Lambrechts & Dhondt (1986); PhyTro: willow warbler, *Phylloscopus trochilus* from Gil et al. (2001); SerCan[1]: canary, *Serinus canaria* from Nottebohm & Nottebohm (1978); SerCan[2]: canary from Leitner & Catchpole (2004); SetRut: American redstart, *Setophaga ruticilla* from Lemon et al. (1994); StuVul: European starling, *Sturnus vulgaris* from Eens et al. (1992a); SylCom: whitethroat, *Sylvia communis* form Balsby (2000); and FicAlb: collared flycatcher from the current study. Sample sizes for each study are given above the effects

focused on males that were older than yearlings. We detected large but negative effect sizes for age-dependent variation in song rate, as yearlings sang at higher rates than older males. In general, the effect size for the relationship between age and song was larger than 0.5, but the associated effect sizes could be estimated with only broad Cis. Age/song correlations in the collared flycatcher support the hypothesis that song is a reliable signal of age, mostly because it helps separate yearlings from older birds. However, the negative relationship found for song rate indicates that song traits are not always more expressed in older males than in yearlings. We found effects of weaker magnitude for the relationship between survival and song, implying that song and age are unlikely to be related due to phenotype-dependent survival. Results for survival do not support the hypothesis that song is a reliable indicator of viability.

Several studies in passerines have demonstrated that yearling males have smaller repertoires than older ones (Fig. 2). This age-dependence is likely to result from new song elements being added to the repertoire sung in the second year of breeding (Nottebohm & Nottebohm 1978; Yasukawa et al. 1980a; Cosens & Sealy 1986; Eens et al. 1992b; Gil et al.

2001), as a consequence of song-learning (Kroodsma 1982), or songs that are memorized but not produced by yearlings (Geberzahn et al. 2002). Differences in song between yearlings and older males can be regarded as a case of delayed maturation, which is generally observed for plumage traits (Cucco & Malacarne 2000). In some species, repertoire size can even differ among older age categories (Yasukawa et al. 1980b; McGregor & Krebs 1989; Lampe & Espmark 1994; Mountjoy & Lemon 1995; Birkhead et al. 1997; Eens 1997), while in others, there seems to be no change after the second year of breeding (Lambrechts & Dhondt 1986; Hiebert et al. 1989; Hasselquist et al. 1996a; Gil et al. 2001; Kipper et al. 2004). In another set of species, studies failed to detect significant relationship between age and repertoire size (Searcy et al. 1985; Catchpole 1986; Bijnens 1988; Lemon et al. 1994; Nordby et al. 2002; Leitner & Catchpole 2004). To make it even more complex, there may be different rules applied in different populations of the same species (Forstmeier et al. 2006). However, the general pattern indicates that in the majority of species, repertoire size is consistently smaller in yearlings than in older males (Fig. 2). The collared flycatcher appears to belong to those species, which show differences in

repertoire size across the whole age spectrum (Tables 2 and 3).

Beside repertoire composition, temporal patterns in the song can also show age-dependent variation (Lambrechts & Dhondt 1986; Loffredo & Borgia 1986; Bijnens 1988; Eens et al. 1992a; Cucco & Malacarne 1999; Galeotti et al. 2001; Garamszegi et al. 2005). However, the importance of different temporal features vastly differs among species. Here, we found strong age-effects for song rate, but these relationships were more robust when comparing yearlings to older males than when focusing on older age differences. Interestingly, song rate tended to be higher in yearlings than in older males. We expected the opposite tendency to occur, as song rate is generally thought to be positively correlated with male quality. We can think of two explanations for the unexpected pattern. First, the high song rate of yearlings may be an attempt to compensate for their small repertoire size (Catchpole et al. 1984; Balsby 2000). Such masking of repertoire size with a higher song rate may be effective, if females sample males in short time windows (see Hiebert et al. 1989). We lack information on how listeners perceive songs, but if such mechanisms were in effect, the augmentation of song rate may reflect an attempt of yearlings to increase their apparent quality. A recent modeling exercise indicated that evolution can favor older males to signal more reliably than yearlings when the chances of reproducing in the future fade with aging (Proulx et al. 2002). Secondly, the high song rate of yearlings may indicate their increased interest in territory defense. In a recent study, we found that yearlings generally showed more aggressive responses toward territory intruders than older males (Garamszegi et al. 2006b). Perhaps, the relationship between age and song rate is a manifestation of the same phenomenon, as song rate can be important in a male–male context (in the collared flycatcher: Garamszegi et al. 2004a; in general: Searcy & Nowicki 2000). Clearly, our correlative results do not reflect causal mechanisms, and we need more experimental data to understand the determinants of the age-dependence of each song feature in the collared flycatcher, which are acting in different ages.

In general, the intermediate effect size for the general relationship between song and age is in accordance with the predictions of theories of sexual selection (Jennions et al. 2001; Kokko et al. 2002). If trait expression is related to male age to some degree, and mating with a male from a particular age class has consequences for female fitness, female preference for the most beneficial age will favor reliable signaling mechanisms of age. In the studied species, mating with older males may confer genetic benefits to females in terms of better offspring development in certain environmental conditions (Hegyi et al. 2006a). Hence, there should be a strong selection for females to avoid mating with young males at the social or extra-pair level. Consequently, age dependent signaling is expected to become important, and song (current study) and plumage traits (Török et al. 2003) will be probably involved. In addition, females seem to invest more testosterone in the egg to compensate for the potentially negative consequences of such costly matings with yearlings (Michl et al. 2005).

If viability is heritable, choosy females preferring attributes that reveal the probability of survival in males can obtain viability genes for their offspring. Although some studies reported that a relationship between song and survival may exist (e.g. Lambrechts & Dhondt 1986), we found weak effect sizes for survival indicating that song has a low potential to reliably signal male viability per se. The relatively weak relationship between survival and song may have implications for the mechanisms of age-dependence of song features. One explanation for the age-dependent variation of sexual traits is that such traits have different survival values. Unfortunately, we did not have longitudinal data of the same individuals to disentangle directly the effects of survival from the effects of within individual changes. At least, the weak relationship between song and survival allows us to speculate that the age-dependent expression of repertoire size and song rate may not result from the phenotype-dependent survival of males. The apparently weak role of survival, together with the overwhelming evidence for the longitudinal increase of repertoires in general (e.g. Nottebohm & Nottebohm 1978; Yasukawa et al. 1980a; Cosens & Sealy 1986; Eens et al. 1992b; Gil et al. 2001), and in the closely related pied flycatcher in particular (Espmark & Lampe 1993), suggests that repertoire size of the collared flycatcher may also show within individual changes.

The findings of this study are based on correlations across individuals, and such approaches have some limitations that warrant attention. First, an apparent relationship between age and song may be mediated by a third, unidentified factor resulting in no causal association between the former two traits. We have examined this possibility by controlling for the potentially confounding effect of year, date and time of recording (results are not shown), and we found that the general relationship between age and song

remained very similar. Secondly, we relied on a moderate sample size giving rise to broad CIs that were associated with our effect size estimations. Our sample sizes and CIs are comparable to what one can reach in behavioral studies in general, and in the study of bird song in particular (see Fig. 2). Therefore, we suspect that the low precision of effect size estimates is a common problem in the behavioral ecology of bird song.

To summarize, we found medium to strong effects for the song of the collared flycatcher being related to male age, but we only detected weak effects for survival. We demonstrated that the underlying mechanisms may be substantially different at different age-transitions and for different song traits. We also showed that age-effects do not necessarily translate into survival effects, because age differences in song are more likely caused by individual changes than by phenotype-dependent survival. Our findings are in accordance with previous findings in other species, and support the hypothesis that song is a reliable indicator of male quality. However, not all features of songs are unequivocally more expressed in older males than in yearlings.

## Acknowledgements

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