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Learn it now, sing it later? Field and laboratory studies on song repertoire acquisition and song use in nightingales

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Abstract In many bird species, song changes with age. The mechanisms that account for such changes are only partially understood. Common nightingales *Luscinia megarhynchos* change the size and composition of their repertoire between their first and second breeding season. To inquire into mechanisms involved in such changes, we compared the singing of 1-year-old and older free-living nightingales. Older males have more song types in common than have 1-year olds. Certain song types frequently sung by older birds did not (or only rarely) occur in the repertoire of yearlings ('mature' song types). We conducted learning experiments with hand-reared nightingales to address reasons for the lack of mature song types. The acquisition success of mature songs was as good as that of control songs (commonly sung by both age groups). However, the analysis of song type use revealed that all yearlings sang common song types more often than mature types. This indicates that the absence of certain song types in the repertoires of free-living yearlings cannot be accounted for by learning and/or motor constraints during song learning. Moreover, our results suggest that in communication networks, animals may restrict the actual use of their signal repertoire to a certain subset depending on the context.

Keywords Song · Nightingales · Vocal learning · Communication · Signal use · Repertoire composition

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Introduction

Vocal learning is a rare trait in the animal kingdom. Besides humans, only very few mammalian vocal learners have been described: cetaceans (Janik and Slater 1997) and pinnipeds (Ralls et al. 1985; Sanvito et al. 2007). Bats and mice are candidate species (Boughman 1998; Knörnschild et al. 2010, 2012; Arriaga and Jarvis 2013), but conclusive evidence (derived, e.g. from tutoring experiments) is still lacking and results are under controversial debate (e.g. Arriaga et al. 2012; Hammerschmidt et al. 2012). In the class of birds, evidence is more conclusive: here, vocal learning has evolved independently in three groups: hummingbirds (Baptista and Schuchmann 1990; Jarvis et al. 2000), parrots (Todt 1975; Pepperberg 1999; Berg et al. 2012) and songbirds learn part of their vocal repertoire by imitation.

Striking parallels between birdsong and human speech learning occur at different levels of this fascinating acquirement (review in Brainard and Doupe 2013): in both systems, learning starts in an early sensitive phase of perceptual learning which finally results in the typical species-specific signals, often with regional dialects (Baker and Cunningham 1985). In humans as well as in many songbirds, a social tutor is important for learning success (Todt et al. 1979). Only later during learning, bird fledglings as well as human babies start to produce own sounds, called soft song or babbling, respectively, and comprises remarkable similarities concerning timing and patterning of these precursors of song/speech. Also, for both, auditory feedback on the produced vocalizations is obligatory for motor control. After song or speech crystallization, the features of the signals remain rather stable, and in both cases, auditory feedback is still necessary for the production. Additionally, the neural and genetic basis for vocal learning in both taxa has been described to consist of amazingly analogue structures and processes (Bolhuis et al. 2010; Scharff and Petri 2011; Scharff and Adam 2013). Thus, birdsong provides a promising model to study the physiological as well as ecological conditions for learning.

Learned vocalizations in songbirds often exhibit age-dependent vocal plasticity throughout life, which can be a result of continued vocal learning or of the differentiated use of a vocal repertoire learned in early ontogeny. Several patterns of change have been described in different songbirds. Age differences do occur not only at the level of repertoire size but also in repertoire composition and element properties (review in Kipper and Kiefer 2010), and at the level of song output. For example, older rock sparrows *Petronia petronia* sing at lower rates and with higher amplitude compared to yearlings (Nemeth et al. 2012). The performance of song structures may also change with age. Syllable-type consistency increases with age in tropical mockingbirds *Mimus gilvus* (Botero et al. 2009), trill notes are sung less variably by older banded wrens *Thryothorus pleurostictus* (De Kort et al. 2009) and older swamp sparrows *Melospiza georgiana* sing trills with higher repetition rate and larger frequency bandwidth ('vocal performance') than younger males (Ballentine 2009). Though it has been suggested that the poorer performance of younger birds may reflect constraints in auditory-guided motor learning as well as motor performance (Podos et al. 2009), and learning experiments in the lab provided evidence that some bird species are truly open-ended learners, i.e. have that capability to acquire new vocalizations after song ontogeny (e.g. Nottebohm et al. 1986; Chaiken et al. 1994; Geberzahn and Hultsch 2003), little is known about learning mechanisms leading to vocal plasticity in the life history of individual birds (review in Beecher and Brenowitz 2005).

The common nightingale is for several reasons a very good model organism to investigate mechanisms of age-dependent changes in learned vocalizations. There exists profound knowledge on learning properties of the species under laboratory conditions (review, e.g. in Hultsch and Todt 2008) as well as age-dependent changes in repertoire size and repertoire composition of birds in nature (Kipper et al. 2006; Kiefer et al. 2006, 2009). Whereas males of 2 years and older contained on average 190 discrete song types (Kipper et al. 2004), repertoires of first year individuals were significantly smaller (Kiefer et al. 2006). Birds of the two age classes also reacted differently to a simulated vocal intruder (Kiefer et al. 2011). When comparing song of individual males longitudinally in their first and second breeding season, it turned out that many song types were no longer sung in year 2, others were added and the repertoire increased overall by 24 % (Kiefer et al. 2009). This reorganization of repertoires led to an increase of song type sharing levels with the breeding population's 'popular' song types in successive seasons (Kiefer et al. 2010). Concerning structural song characteristics, buzz elements revealed no differences between 1-year-old and older birds when only comparing same buzzes in a longitudinal approach (Weiss et al. 2012), whereas the general performance of trill songs differed between age groups (cross-sectional comparison on overall trills, Sprau et al. 2013). Furthermore, a recent study did show that patterns of song sequences differ between 1-year-old and older males (Weiss et al. 2014).

Tutoring experiments conducted on hand-reared males in the laboratory corroborate the findings on song repertoire changes from the field: (1) Even though nightingales have a sensitive phase for auditory learning early as fledglings (Hultsch and Kopp 1989), males also add new song types after later exposure close to song crystallization, i.e. during their first breeding season (Geberzahn and Hultsch 2003; Todt and Geberzahn 2003); (2) As with nightingales in the field, hand-reared males increased the size and composition of song type repertoires produced in their first singing season and both variables tended to be stable from their third year onwards (Wistel-Wozniak and Hultsch 1993).

So far, learning properties have mostly been investigated under laboratory conditions. Only few studies used an experimental approach in the field (Eriksen et al. 2009; Eriksen et al. 2011) or a combination of laboratory with field work (O' Loghlen and Rothstein 2012).

We addressed whether learning constraints may be the reason why certain songs are not sung in the field by a combined analysis of song under natural conditions in the field with a learning experiment under controlled conditions. In a first step, we carried out a field study where we compared the composition of song type repertoires of 1 year and older males. In particular, we examined whether the occurrence and frequency of shared song types shows a different distribution in the two age classes. In addition to the occurrence of song types, we also analyzed how often younger or older males used certain song types, because differential use may be indicative of functional age-related aspects in the communication network of a population. This comparison revealed that certain song types frequently sung by older birds were not present in the repertoires of 1-year-old birds. Based on this finding, we conducted a song learning experiment under controlled conditions to study whether the specific profile of repertoire composition of 1-year-old birds (in the field) may be a consequence of learning constraints. We hand-reared fledglings and conducted tutoring experiments in order to examine whether motor and/or learning constraints would account for the absence of certain song types in the repertoires of 1-year-old males, as suggested by the field data. Therefore, we tutored males with two treatments: song types that did rarely ('mature') or commonly ('common') occur in the singing of 1-year males in the field. If learning constraints account for the lack of certain song types in 1-year olds, then males should acquire and copy mature song types not as good as common ones. General learning but different use would rather point to a context-dependent deployment of song.

Methods

Repertoire comparisons of age classes

Subjects and study site

In the framework of a long-term field project on male nightingale singing behaviour and breeding ecology in the Treptower Park, Berlin (Germany), territorial nightingales have been recorded and colour-banded since 2001 with the permission of the Senatsverwaltung für Stadtentwicklung und Umweltschutz and on behalf of the Vogelwarte Radolfzell (Max-Planck-Institute for Ornithology). Age (first breeding season or older) was determined by subtle feather features (Glutz von Blotzheim and Bauer 1988; Svensson 1992; Mundry and Sommer 2007). For the present study, we analyzed the spontaneous nocturnal song of six 1-year-old and six older nightingales. Subjects of both age classes were spaced throughout the study site. We recorded at least 1 h of nocturnal song using Sennheiser ME 80/K3U or ME66/K6 directional microphones with windbreak, and a Sony TCD 5 tape recorder, Sony WMD 6 walkman or a Marantz PMD 660 solid state recorder. Though using different equipment may introduce variation in recordings, for the purpose of our study, this was not relevant as nightingales sing their song types with high stereotypy and element properties are very discrete (see below; further illustrations in Kipper et al. 2004; Kiefer et al. 2010).

Analysis of song, data analysis and statistics

For all song analyses, we used the programme Avisoft-SASLab Pro 4.38 (R. Specht, Berlin). Where necessary, we digitized analogue recordings (44,100 Hz, 16-bit resolution). Spectrograms were printed and visually analyzed (settings: sample rate=22,050 Hz, FFT=256 points, Hamming-Window, overlap 50 %). For each bird, we compared the song type repertoires based on analyses of 533 consecutively produced songs (equivalent to about an hour singing). For the comparison of repertoires, we applied criteria described in Hultsch and Todt (1981). The high stereotypy of song type performance within and between individuals allows a reliable determination of the song type repertoire for each bird and a comparison of repertoires across birds (for spectrogram examples, please see Kiefer et al. 2010, Fig. 1).

In order to compare song type sharing among birds of the two age groups, we determined the amount of song type sharing among 1-year-old (n=6: 2005 (3), 2006 (3)) and older birds (n=6: 2005). We used repertoire analyses from a previous study (Kiefer et al. 2010) to calculate the number of shared song types of one male with all other males within its age group (median) for both age groups. In order to determine the influence of age and of (the possibly confounding) repertoire size on sharing levels, we fitted a generalized linear model with age and repertoire size as fixed factors and median of shared song types with birds own age class as response variable by using Poisson error distribution (R 2.14, R Development Core Team 2009).

In addition, we determined (separately for age groups) how many song types were shared by all six, five, four…. males and how many song types were uniquely sung by individual birds. In addition to these parameters on repertoire composition and sharing, we determined song type use by counting how often each song type was sung by each individual within a sequence of 533 consecutive songs.

For the present study, we focused on two song type sets, classified based on their occurrence in repertoires. To do so, we analyzed which song types occurred in one age group but not in the other one. Song types only found in older, but not in 1-year-old birds, we termed *mature* and those occurring in both age groups we termed *common* song types. There were no song types that occurred only in repertoires of 1-year-old birds. Considering the small sample of six birds per age group, the classification had to be treated cautiously. To further corroborate the classification of mature and common song types, the findings based on these 12 birds served as a standard for a follow-up comparison of more birds from both age groups recorded in following years. For this additional data set, we restricted repertoire analysis to checking whether mature and common song types found in our initial sample occurred in the repertoires of another 6 1-year-old birds and 12 older birds.

Learning experiments

Subjects

As part of a project on song learning and song preference learning in male and female nightingales, we collected four nests with freshly hatched nightingales at the end of May 2006 (permitted by the Senatsverwaltung für Stadtentwicklung der Stadt Berlin nach §43 (8) BNatSchG). Nestlings had an age of 3–6 days (i.e. before the beginning of their sensitive phase of song acquisition; Hultsch and Kopp 1989; for details of housing, see Online Resource 1).

Tutoring

Based on the analysis of singing of 1-year-old and older birds and the classification of common and mature song types, we tutored six hand-reared males with three different stimulus strings each consisting of 8 song types: either only common, only mature or a mix of common and mature song types (four renditions of each category; Fig. 1). In order to compare the acoustic structure and complexity of common and mature tutor song types, we determined the following measures for

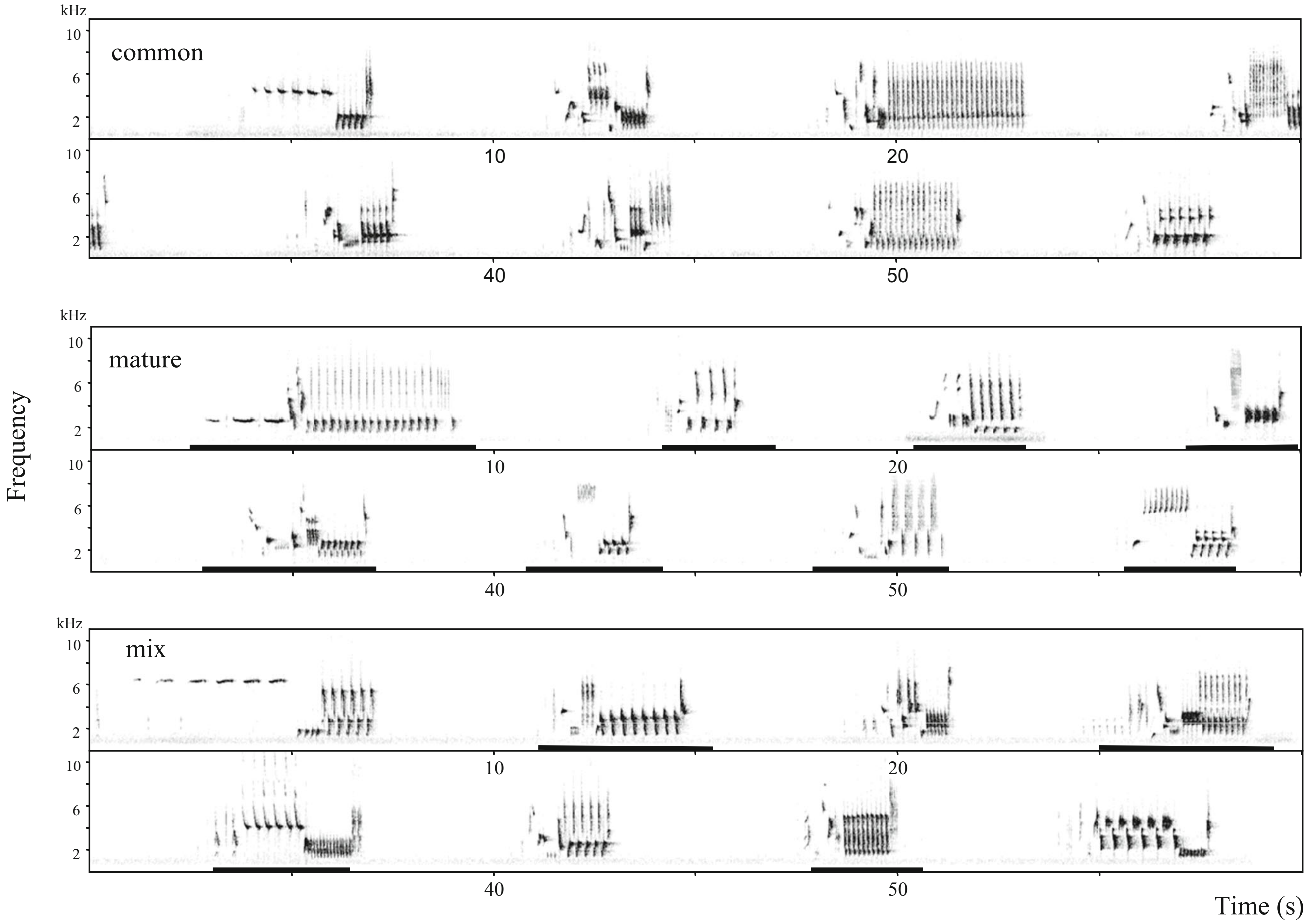


Fig. 1 Illustration of tutored songs: three strings of tutoring song types (common, mature and 'mix'—*black lines* indicate mature song types, for details, see 'Methods'). There were no overt acoustic differences among the song categories mature and common

each tutor song: song length, minimum frequency, maximum frequency, peak frequency at maximum amplitude, number of elements, number of different elements and the relation of number of elements/number of different elements. Measures were averaged for the three tutoring examples of each song type. None of the measures differed between common ($N=12$) and mature ($N=12$) songs (Mann–Whitney U test, $N_1=N_2=12$, all $P>0.05$). Thus, none of these measures was likely to account for mature song types not being sung by younger birds.

Songs for the tutor strings were chosen from high-quality recordings (with little background noise) from nocturnal song of three nightingales of a Berlin population approx. 12 km away from the nesting sites. The song type strings were compiled with the programme Avisoft SAS Lab Pro (version 4.38, R. Specht, Berlin, Germany). From these recordings, we copied the song types to be presented as song models, filtered background noise (high pass 0.7 kHz, filter-type Butterworth, order 8), normalized all song types separately (75 % volume) and, finally, assembled them in randomized order. Between each song type, we inserted pauses of 4 s which is in the typical range of intersong intervals in nightingale singing.

We randomized the order of string presentation. On each day, we presented each of the three strings three times in a row, separated by 30 s of silence. The intervals between presentations of the three string categories were set to 45–60 min. We daily repeated this procedure in randomized order for 9 days (e.g. at the first day: 1. common 3×, 2. mature 3×, 3. mix 3×), resulting in a total of 27 exposures to each string (and song type). Tutoring frequencies within this range are sufficient for learning in nightingales (review in Hultsch and Todt 2008). Strings were played through loudspeakers positioned in front of the human 'social tutor', whose presence enhances song acquisition success during the early sensitive phase (Todt et al. 1979). Stimuli were played back as wav files with a portable CD-player (Sony D-EJ611) connected to a Sony SRS-A205 loudspeaker. Amplitude was adjusted to natural song (approx. 75 dB at a distance of 1 m to the loudspeaker; Brumm 2004) measured with a precision sound level meter (CEL 314, time constant 125 ms). The males were 14 to 17 days old when the tutoring started, i.e. at the beginning of their first sensitive phase of auditory song learning (Hultsch and Kopp 1989).

Song analysis

The singing of the six males was automatically recorded (24 h/day) throughout the first 2 years (microphones Sennheiser ME66 or Earthworks TC20 connected to a computer). Recordings were done with the programme Sound Analysis Pro SAP (Tchernichovski et al. 2000). Tutor song acquisition was determined using recordings of crystallized song (April–May 2007). To determine the learning success (i.e. which of the stimulus songs had been acquired as imitations), we analyzed on average 364 (range 96–736) songs in recordings from early to mid May. In previous studies, this number had been shown to be sufficient to determine the individual learning success (Hultsch and Todt 1989). Spectrograms of song recordings (programme Avisoft-SASLab Pro 4.40; R. Specht, Berlin; settings: as above) were compared by visual inspection to tutor song types.

We determined the learning success of mature song types (in percent: number of learned mature song types × 100/12) and common song types (in percent: number of learned common song types × 100/12) for each individual. Additionally, we counted how often each song type was sung. To test whether imitations of one category (mature or common) were preferentially used over the other, we calculated the use of song types of the two categories in relation to the learning success (for details of this calculation, see Online Resource 2).

As measures of song performance, based on the same recordings, we determined the following measures for the songs learnt: song length, minimum frequency, maximum frequency and peak frequency at maximum amplitude. For the song types sung most often by most birds, we additionally determined the number of elements and number of different elements. From the latter, we calculated the difference to the number of different elements of the respective tutor songs.

For all these measures, we first calculated a mean and standard deviation (as a measure of song variability) for each song type and each bird. In order to have a single measure of these parameters and their consistency, we afterwards averaged these parameter values per bird. Finally, differences in these measures were tested using Wilcoxon signed rank tests.

Results

Comparisons of age classes in free-ranging males

We first analyzed the sharing of song types among 1-year-old and older birds. Pairs of 1-year-old nightingales shared on average 58±15 (mean±SD) song types (repertoire size 131±31), whereas in older birds, sharing was much higher (110±17 song types; repertoire size 168±32). Older birds did not only have larger repertoires but also had more song types in common than did 1-year-old males (GLM using Poisson error distribution; age group estimate=0.564, SE=0.077, z value=7.306, $P<0.001$; repertoire size estimate=0.002, SE=0.001, z value=2.116, $P=0.034$; method as in Faraway 2006; Zuur et al. 2009; Fig. 2). This evidence for age differences in song sharing was further supported when inspecting sharing matrices, where we did not see any indication for individually biased sharing levels.

Next, we compared the repertoire composition of six 1-year-old and six older birds. Twenty song types were not sung by 1-year-old birds (mature song types). In order to get a balanced data set, we searched for 20 song types that all birds of both age groups sang (common song types). Older birds sang mature song types as frequently as common ones (exact Mann–Whitney U test, $N_1=N_2=20$, $U=196$, $P=0.92$). In order to corroborate this outcome, we enhanced the sample size and analyzed more repertoires from breeding seasons in following years. The initial results were verified by the follow-up analysis: here too, 1-year-old birds had fewer mature song types in their repertoires (11±2 versus 13±2 mean±SD; exact Mann–Whitney U test, $N_1=N_2=18$, $U=57.5$, $P=0.000$). In

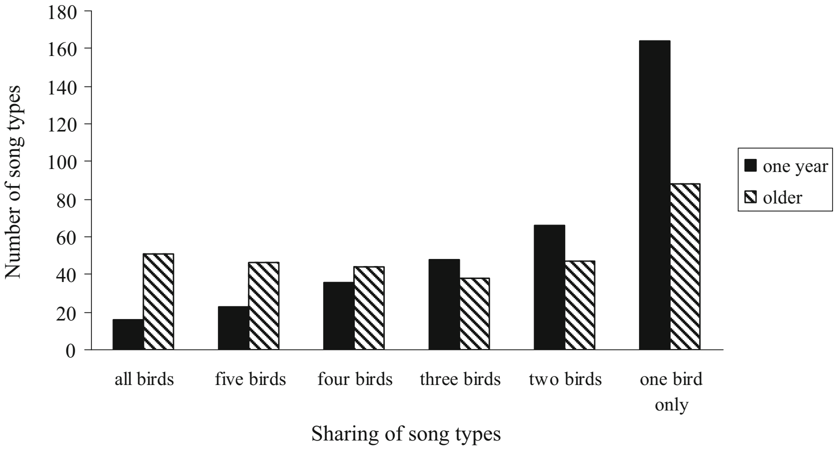
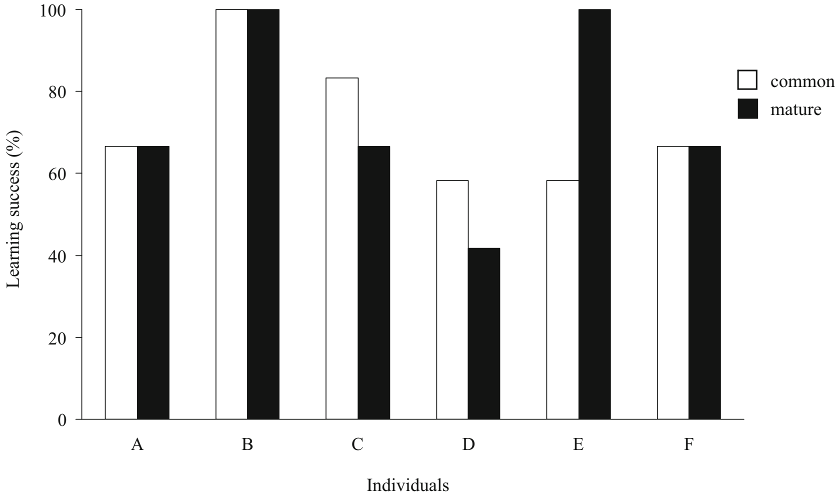


Fig. 2 Summed number of song types (y-axis) that were shared by a certain number of males (x-axis) of two age groups in a Berlin population (1-year-old, $N=6$, 2005 and 2006, each $n=3$; older birds, $N=6$, 2005). See 'Methods' for details. Older birds had more song types in common than 1-year-old birds

Fig. 3 Learning success (%) for common and mature song types of six male hand-reared nightingales. Acquisition did not differ between the two categories



addition, mature song types were sung less often by 1-year-old birds than common ones (exact Mann–Whitney *U* test, $N_1=N_2=18$, $U=71$, $P=0.003$). There was no difference in the occurrence (exact Mann–Whitney *U* test, $N_1=N_2=18$, $U=122.5$, $P=0.09$) and use (exact Mann–Whitney *U* test, $N_1=N_2=18$, $U=116$, $P=0.15$) of mature and common song types of 12 older birds.

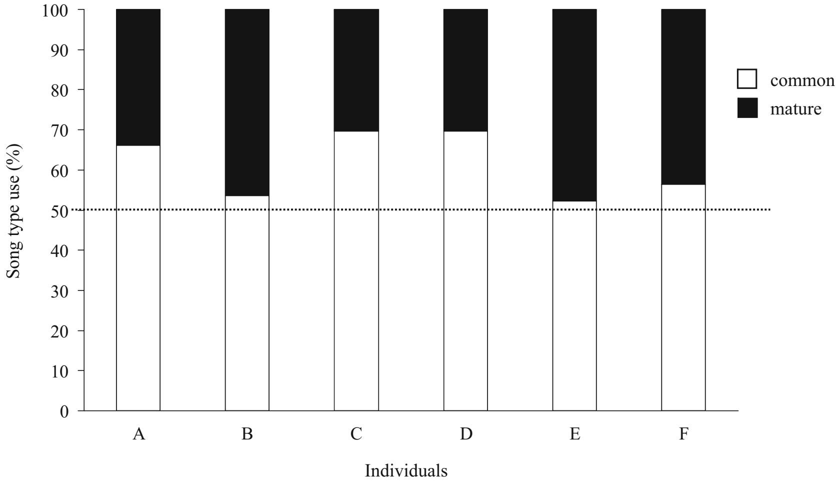
Results of learning experiments

All nightingales imitated mature and common song types, and the percentage of learnt songs did not differ among the two categories (exact Wilcoxon signed rank test, $N=6$, $T^+=3$, $P=1.0$, Fig. 3). However, all males sang common song types more frequently than mature song types (exact Wilcoxon signed rank test, $N=6$, $T^+=21$, $P=0.03$, Fig. 4). Concerning the measures of song performance (song length, minimum frequency, maximum frequency, peak frequency at maximum amplitude, number of elements and number of different elements), there were no differences between mature and common song types (tested for mean values per song type per bird and for standard deviation as a measure of song consistency; Wilcoxon signed rank tests, all $N=6$, $V>3$, $P>0.05$). Similarly, the comparison of common and mature song categories revealed no difference in the number of element types in acquired and tutor songs (again tested for mean and standard deviation per bird; Wilcoxon signed rank tests, both $N=6$, $V>11$, $P>0.05$).

Discussion

Our study confirmed that yearling nightingales have smaller repertoires than older birds and we found that they shared fewer song types with each other than do older birds. Certain song types were rarely if ever sung by yearlings. In a learning experiment, these song types were learned by hand-reared males but not used very often in song.

Fig. 4 Use of imitations of common and mature song types (%) in the song output of six hand-reared males. The *dashed line* indicates a singing of the two song categories at chance rates, i.e. on a 50:50 chance level. For details, see 'Methods'. All males sang common song types more often than mature song types



Our results on the repertoire composition of young birds are in line with previous studies that demonstrated that repertoires of yearling nightingales are changed and expanded by the second season (Kiefer et al. 2009, 2010) and that 1-year-old birds share less with their breeding population than do the same birds in their subsequent year (Kiefer et al. 2010).

Whether the existence of 'mature song types', i.e. those that are not sung by 1-year olds, can be explained by learning constraints was tested in a song tutoring experiment. In this experiment, song types of the category mature were readily learned by the hand-reared birds: males acquired mature song types to the same degree as the control songs (common song types). As all males learned both categories to the same amount, physiological or learning mechanisms do not seem to account for the lack of certain song types in the repertoires of yearlings in the field. But, similar to free-ranging yearlings, the hand-reared birds *used* mature song types less often than common song types. They did so even though they heard both categories equally often during tutoring. Thus, differentiated use rather than general learning constraints seems to be the explanation for the occurrence of mature song types only sung by older males.

In the following, we present possible explanations for these findings. From a functional point of view, younger males may benefit from the avoidance of singing certain song types. This behaviour might signal their inferiority in order to avoid aggression (Rohwer 1978). Playback experiments proved that birds can indeed differentiate acoustically between age groups (Osiejuk et al. 2007; De Kort et al. 2009; Kiefer et al. 2011; Poesel and Nelson 2012). Also, Cucco and Malacarne (2000) considered whether song changes might be due to a process called delayed maturation described also for morphological features (plumage). Mechanisms that may account for the lack of certain song types in the repertoire and repertoire deployment of yearling males might be neurobiological and/or motor constraints. Some studies did report differences in singing and neuronal substrates underlying song learning for different age groups (e.g. Bernard et al. 1996; MacDougall-Shackleton et al. 2005; Wilbrecht et al. 2006). Additionally, it might be that mature song types require more experience in the learning process in order to produce them properly. Although in our tutoring experiment we found no differences between the song categories mature and common with regard to the song complexity measures we analyzed, the mature category may still consist of songs with more challenging song characteristics and, thus, might reflect male quality. For example, these song types may be potentially of higher performance than others. Two studies on other species emphasize this idea: 1-year-old swamp sparrows sing with lower song performance than older birds (Ballentine 2009), lower performance here being expressed in lower trill rates accompanied by lower frequency bandwidths. Also, banded wrens improve performance features with age by increased trill consistency (De Kort et al. 2009). If renditions of the two categories differ in the consistency of parameters (i.e. mature song types are more variable than common song types), then the former category is a candidate to reveal performance cues. Our analyses of song consistency of the two categories do not hint in this direction, but there might be other characteristics which impair the potential for such cues. Then, younger males may avoid singing them despite the fact that they are able to do so, thereby avoiding a direct comparison to the performance of older birds. This hypothesis can be examined in a future playback study, presenting low- and high-performance versions of mature song types in the playbacks. If performance characteristics of mature song types would be revealing the age or actual state of the sender (review in Searcy and Yasukawa 1996), yearling nightingales are expected to avoid answering to songs of higher performance with matching responses, as suggested by Logue and Forstmeier (2008).

To summarize, this study confirmed that there exist profound differences in repertoire size, sharing and composition of 1-year-old and older nightingales. The occurrence of mature song types does not seem to be a consequence of learning constraints. However, some intrinsic mechanisms seem to affect a differentiated use of song types: even with the same amount of tutoring and without social reinforcement, mature song types were not sung as often as common song types. We suggest that performance constraints are a candidate explanation for this finding.

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