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Tuning towards tomorrow? Common nightingales *Luscinia megarhynchos* change and increase their song repertoires from the first to the second breeding season

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In many oscines, song repertoire size correlates with male quality and female mate choice, and can vary with age. In a cross-sectional field study in common nightingales *Luscinia megarhynchos*, one y old birds had substantially smaller repertoires than did older ones. In laboratory experiments males can acquire new song types during this period. This longitudinal field study therefore investigates whether individual nightingales increase their repertoires from the first to the second breeding season. We report a striking repertoire turnover, with an average overall increase of 24% of the first season's repertoire, resulting from added and dropped song types (54% and 30%, respectively). The number of added song types correlated positively with the size of the first season's repertoire. These results are consistent with the notion that repertoire size in nightingales correlates with male quality, although the overlap between repertoire sizes of first and second season birds makes it impossible to discriminate age based solely on repertoire size. Comparing the number of song types an individual sang in both seasons ('permanent song types') revealed a lower overlap than reported for subsequent seasons. The frequencies with which these were sung in the first season were less predictive of how often they were sung in the second season than was the case between later years. This drastic repertoire turnover from the first to the second season may be a selective process in response to the local song types, constrained by genetic makeup and shaped by early experience.

Birdsong is a communicative signal that evolved through sexual selection and is used in intra- and intersexual interactions. Different species use different properties of acoustic signals on several song hierarchy levels to encode, convey, and extract information (review in e.g. Marler and Slabbekoorn 2004). Large and variable song repertoires may be a form of exaggerated signaling with potentially high costs, the 'peacock's tail' of bird song (Catchpole and Slater 2008). How exactly the information that is used in interactions and mate choice is encoded in large repertoires is poorly understood. Repertoire size is positively correlated with male quality measures such as higher lifetime reproductive success (great tit *Parus major*, McGregor et al. 1981; song sparrow *Melospiza melodia*, Reid et al. 2005), territory quality (great reed warbler *Acrocephalus arundinaceus*, Catchpole 1986), parental care (sedge warbler *Acrocephalus schoenobaenus*, Buchanan and Catchpole 1999), nestling condition (great reed warbler, Nowicki et al. 2000), and/or reduced infection with parasites and/or increased immunity against pathogens (sedge warbler, Buchanan et al. 1999; barn swallow *Hirundo rustica*, Garamszegi et al. 2005). These relationships between repertoire size and quality measures have been investigated mostly in species with small to medium sized repertoires. In common nightingales *Luscinia megarhynchos* which possess large song type repertoires (about 190 song types per adult male, Kipper et al. 2004), the spring arrival date from winter quarters as well as body size at the onset of the breeding season are positively correlated with song repertoires (Kipper et al. 2006).

One way to address the function of exaggerated signals such as very large song repertoires is to study their development over the lifetime of individuals. Many sexually selected signals change over an individual's lifespan. This could in turn reflect the quality of individuals, with older males having acquired more experience (reviewed in Martin 1995), or proving their higher quality by their longevity (reviewed in Brooks and Kemp 2001). Accordingly, identifying and choosing more mature mates might be advantageous for females, and males likewise might base their agonistic interactions by judging age through song.

Variation in repertoire size and organization might also reflect an adjustment of one's repertoire to the songs sung in the breeding population. Several song bird species change their repertoires, resulting in increased song sharing among neighbours (American redstarts *Setophaga ruticilla*, Lemon et al. 1994; willow warblers *Phylloscopus trochilus*, Gil et al. 2001; sedge warblers, Nicholson et al. 2007;

thrush nightingales *Luscinia luscinia*, Grießmann and Naguib 2002). This is assumed to be advantageous in male-male encounters and territory tenure (Beecher et al. 1996, 2000a,b, but see Wilson and Vehrencamp 2001, Hughes et al. 2007).

Behaviour in different age classes can be compared either cross-sectionally or longitudinally (e.g. Forstmeier et al. 2006). Cross-sectional studies analyze signal characteristics of different individuals in different age classes, whereas longitudinal studies address signals of the same individual at different ages. Descriptions of age-related changes in signal quality based on cross-sectional comparisons can be difficult to interpret (Gil et al. 2001, Forstmeier et al. 2006), because they can reflect different mortality rates of birds with a certain quality or quantity of a trait. In these cases, differences would not reflect the development of the signal in individual birds, but pre-existing individual variation that is related to different mortality rates. On the other hand, differences in cross-sectional comparisons might indeed reflect changes of the signal with age. There are only few studies which applied both, cross-sectional and longitudinal methods (Gil et al. 2001, Garamszegi et al. 2005, Forstmeier et al. 2006), and these demonstrate the limited validity of cross-sectional analyses. Results from cross-sectional studies revealed that repertoire size was different between age groups in great reed warblers (Hiebert et al. 1989) and song sparrows (Hasselquist et al. 1996), and longitudinal studies indicated that these differences were due to different mortality rates in these species (Searcy et al. 1985, Catchpole 1986). Hence, ultimately, only longitudinal observations of individuals can distinguish between these possibilities.

A longitudinal comparison of repertoire characteristics of nocturnal song of older male nightingales (i.e. in their second breeding season or older) revealed that repertoire size and repertoire characteristics remained stable over years but differed strikingly between individuals (Kipper et al. 2004). In contrast, in a cross-sectional study one-year old birds (i.e. in the first breeding season), had significantly smaller repertoires than older birds (Kiefer et al. 2006). In the present study, we are able to bridge the gap between those findings by comparing repertoire sizes of individual birds longitudinally between the first and second season. In addition, we compare this dataset with a longitudinal dataset of birds which were at least in their second breeding season or older when first recorded. Based on the findings of the two studies mentioned above, we assume that birds will increase their repertoire sizes between season one and two by adding new song types.

Methods

Subjects and study site

We have recorded and colour-banded territorial nightingales since 2001 as part of a long-term field project on nightingale song organization and behavioural ecology in Treptower Park, Berlin (Germany). The park contains typical nightingale breeding habitats, including grassy meadows, bushes, shrubs, wooded areas, a river, small channels and a pond. We captured males with mist nets and song playback three or more days after their 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. Age was determined on the basis of characteristic feather features (Svensson 1992, Mundry and Sommer 2007).

We recorded nocturnal song from the majority of nightingales in the study site (~30 males) 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. Between 2001 and 2006, six birds were recorded in their first and subsequent breeding seasons: Years of first recording were 2003 (two birds), 2004 (one bird) and 2005 (three birds).

Analysis of song type repertoires, data analysis and statistics

We used the program Avisoft-SASLab Pro 4.38 (R. Specht, Berlin) for all acoustic analyses. Analogue recordings were digitized (44,100 Hz, 16 bit resolution) and down sampled to 22,050 Hz. Song spectrograms (settings: FFT = 256 points, Hamming-Window, Overlap: 50%) were then printed and visually analyzed. Nightingales sing with immediate variety. The high stereotypy of song type performance within (and among) individuals allows reliable comparisons within and between recordings. Accordingly, by visual comparison we determined the song type repertoire for each bird applying the criteria suggested in Hultsch & Todt (1981). We assigned songs as belonging to the same song type when they included the same repetitive sections and differed in not more than three of approximately ten element types in the first two sections of a song.

For each bird in each year, we analyzed a sequence of 563 complete and unambiguously identifiable songs, yielding repertoire curves reaching saturation. This was the number of songs in the shortest sequence recorded. For all calculations we used this sequence of 563 songs which corresponds to a singing bout of approximately 60 min. It might be that very few song types of a repertoire were not contained in this sequence but analyses of an even smaller number of songs had in prior studies proven to be sufficient to uncover differences in repertoire size and composition (Kipper et al. 2004, Kiefer et al. 2006). In addition to repertoire size, we determined the number of song types that occurred only in the first season, only in the second season, and in both seasons (hereafter referred to as permanent song types). To obtain a measure of repertoire turnover and similarity of repertoire composition in the two seasons, we calculated DICE-coefficients C_D (with $C_D = 2 \times \text{number of permanent song types}/(\text{repertoire size season } 1 + \text{repertoire size season } 2)$). This coefficient can reach values between zero and one, with zero indicating no permanent song types between two repertoires and one indicating identical song type repertoires.

Furthermore, we analyzed whether birds dropped a significant amount of song types from season one to two. That is, whether birds sang more song types in their first season only (but not in their second one) than expected by chance. We did this using a Monte-Carlo simulation (Adams and Anthony 1996, Manly 1997), applied to each bird's song separately. In this simulation we randomly selected songs from the sequence of the first season, with the number of songs selected equaling the number of songs in the second season's sequence being of types that also occurred in the first season. Then we counted how many first season song types were not within this sample. In order to derive the expected probability distribution of the number of dropped song types we repeated this procedure 1,000 times, each time noting the number of song types not within the sample. The one-tailed P-value assigned to the null-hypothesis that the number of dropped songs did not exceed random expectation was estimated as the proportion of randomisations in which the number of dropped song types was at least as large as in the original sequence. When this P-value was close to the critical threshold of 0.05 we repeated the procedure using 10,000 randomisations.

As a measure of similarity in repertoire delivery, we correlated the frequency of song types in the recordings of both seasons using Spearman's rank order correlation coefficient, including only song types that occurred at least once in each of the two years. A large correlation coefficient indicates that most song types were performed with similar frequencies in both seasons.

Some of the results of these comparisons between breeding season one and two were compared to a longitudinal dataset of nightingale song obtained in two successive breeding seasons where birds in the year of their first recording were in their second breeding season or older (for details see Kipper et al. 2004).

We applied non-parametric, two tailed tests throughout. Small sample sizes required exact versions of most statistical tests (Mundry and Fischer 1998), which were calculated using SPSS. 15.0.1 or a program written by one of the authors (RM) in case of correlations.

Results

The repertoire size of all birds increased from season one ($X \pm SD = 140 \pm 32$ song types,) to season two (172 ± 37 song types) by an average of 32 songs or 24% of the first season's repertoire size (Wilcoxon signed ranks test; $T^+ = 21$, $n = 6$, $P = 0.03$, Fig. 1). Repertoire sizes were correlated between the seasons (Spearman's rank correlation: $r_S = 0.88$, $n = 6$, $P = 0.034$), indicating that birds with a relatively large repertoire in their first season had a large repertoire in their second season, too. Accordingly, individual differences in repertoire size remained relatively stable over seasons. Birds with larger repertoires in the first season sang more new song types in the second season ($r_S = 0.89$, $n = 6$, $P = 0.033$). However, the net gain in repertoire size (i.e. the difference between new and dropped song types) from the first to the second breeding season was not related to the repertoire size in the first season ($r_S = 0.26$, $n = 6$, $P = 0.66$) nor was the relative increase in repertoire size (increase in repertoire size/repertoire size in the first season; $r_S = -0.03$, $n = 6$, $P = 1$).

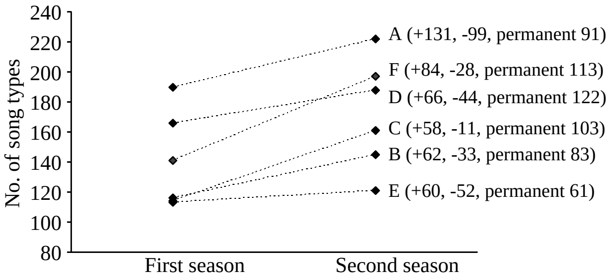

Figure 1. Repertoire sizes of nightingales in their first and second breeding season ($n = 6$). Each subject is represented by a pair of diamonds connected through a dashed line. In parentheses: the number of new (+), dropped (−), and permanent song types of six subjects (A to F).

Concerning repertoire composition, the proportion of songs that were permanent in first and second season repertoires was low compared to the same measure for birds that were at least in their second breeding year (Mann-Whitney U test: $U = 0$, $n_{\text{first year}} = 6$, $n_{\text{older}} = 9$, $P < 0.001$; Fig. 2). The relatively low overlap between first and second season repertoires was not only due to the addition of new song types ($X \pm SD = 77 \pm 28$) but also to a dropping of song types (45 ± 30) from the first season's repertoire. In fact, five out of six birds sang fewer song types than expected by chance from their first season's repertoire in their second season (Monte-Carlo simulation: all $P < 0.005$; 1,000 simulations). Only one subject did not sing fewer song types than expected by chance ($P = 0.15$, 10,000 simulations). Concerning repertoire performance, those song types that were dropped from the repertoire in the second season were on average less frequently sung in the first season than those that were kept in the repertoire (Fig. 3).

When comparing how often each individual sang songs that were present in both seasons we found a significant positive correlation between song type frequencies in the two seasons in one subject ($r_S = 0.20$, $n = 103$, $P = 0.047$, no error level adjustment applied), a tendency for a positive correlation in a second bird ($r_S = 0.21$, $n = 83$, $P = 0.061$), and no obvious correlation in the other four birds (all $r_S < 0.12$, all $n > 61$, all $P > 0.21$). In contrast, the frequencies of permanent songs in subsequent

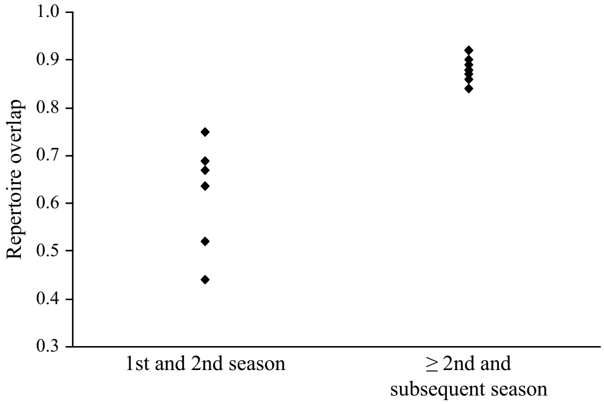

Figure 2. Repertoire overlap between successive years for birds recorded in their first and second breeding season (left, $n = 6$) and birds having been at least in their second breeding season when recorded first (right, $n = 9$). Indicated are DICE-coefficients (for calculation see methods). Each diamond represents one subject.

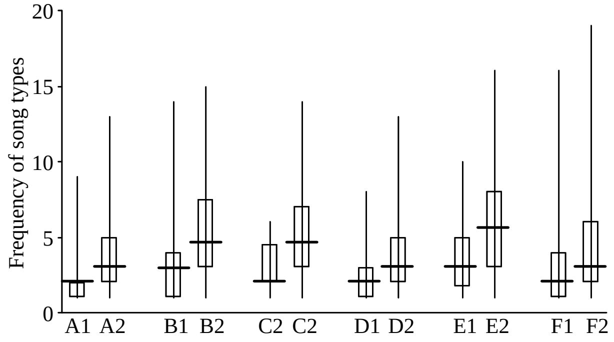

Figure 3. Frequency of song types sung in the first breeding season, plotted for each of the six subjects (A to F): Song types that occurred only in the first breeding season (left bar within subject) and song types that occurred in both seasons (right bar). Each subject sang song types that occurred only in the first season less frequently than song types that it sang also in the second season (Mann-Whitney U tests; A: $n_{1st\ year\ only} = 99$, $n_{both\ years} = 91$, $U = 2633.5$, $P < 0.001$; B: $n_{1st\ only} = 33$, $n_{both\ years} = 83$, $U = 872.0$, $P = 0.002$; C: $n_{1st\ year\ only} = 11$, $n_{both\ years} = 103$, $U = 302.5$, $P = 0.010$; D: $n_{1st\ year\ only} = 44$, $n_{both\ years} = 122$, $U = 2063.5$, $P = 0.022$; E: $n_{1st\ year\ only} = 52$, $n_{both\ years} = 61$, $U = 902.0$, $P < 0.001$; F: $n_{1st\ year\ only} = 28$, $n_{both\ years} = 113$, $U = 915.5$, $P < 0.001$; no error level adjustment applied). Indicated are median, quartiles, minimum and maximum.

seasons in older birds were significantly positively correlated (Mann-Whitney U test: $U = 0$, $n_{first\ year} = 6$, $n_{older} = 9$, $U = 1$; $P < 0.001$; Fig. 4).

Discussion

Our study revealed that the repertoires of nightingales increased substantially between their first and second breeding season. This finding affirms and extends the results of a cross-sectional study on differences in repertoire sizes between first season and older nightingales (Kiefer et al. 2006). In that study it was impossible to distinguish whether differences between first season birds and older birds reflected differences in survival rate between males with different repertoire sizes or an actual increase in individual's repertoire size from the first to the second season (Kiefer et al. 2006). Our study provides evidence that the latter is indeed the case.

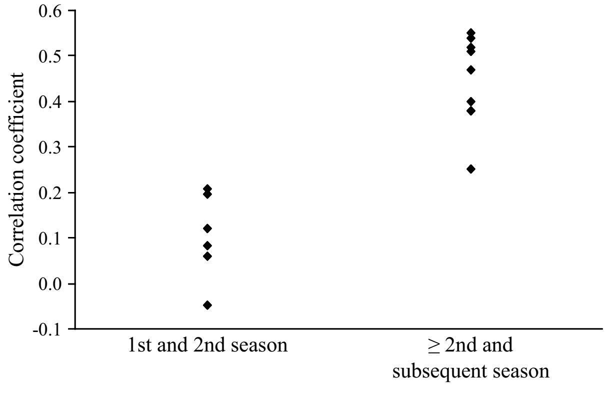

Figure 4. Similarities in frequencies of occurrence with which subjects sang song types that occurred in two successive years for birds recorded first in their first breeding season (left, $N = 6$) and birds having been at least in their second season when recorded first (right, $N = 9$). Each diamond represents the Spearman's rank correlation coefficient calculated for one subject, including only song types sung in both years.

In several song bird species, age correlates with quality (reviewed in Brooks and Kemp 2001). Repertoire size of nightingales from the same population as investigated here was correlated with body measures and date of arrival after migration (Kipper et al. 2006). These features might reflect male quality or seasonal reproductive performance, as shown e.g. for American redstarts (Smith and Moore 2005). Our results also indicate that birds with relatively small repertoire sizes continued to have relatively small repertoires even after adding songs in the second season. A corresponding study of older nightingales showed that relative repertoire sizes remained stable over years (Kipper et al. 2004). Taken together, these results suggest that an individual's repertoire size is constrained, perhaps through genetic quality and/or through parental investment early in ontogeny (Nowicki et al. 2000).

In a previously published cross-sectional comparison of repertoire sizes of first season and older nightingales we reported that these two age classes can rather reliably be discriminated by repertoire size (Kiefer et al. 2006). However, in our current study we instead found a considerable overlap between first and second season repertoire sizes. It seems unlikely, though, that this discrepancy is due to methodological differences since neither first season repertoire sizes nor that of older nightingales differed between our current and the previous study (Mann-Whitney U tests, both $U \geq 17$, $n_{Kiefer\ et\ al.\ 2006} = 9$, $n_{this\ study} = 6$, both $P > 0.25$). The fact that here we investigated birds in their second season, whereas Kiefer et al. (2006) investigated 'at least two years or older birds' is also unlikely to be the cause of this discrepancy since another longitudinal study revealed no changes in repertoire size in nightingales after their second season (Kipper et al. 2004). From our current knowledge it thus seems that the discrimination of one year old from older nightingales based on their repertoire size alone is not as clear-cut as previously thought (Kiefer et al. 2006).

The nightingales in our study did not only change their repertoires between the first and the second breeding season due to an addition of new song types but also through dropping a considerable amount of their first season's song types. In contrast, older nightingales do not change repertoire composition between successive years (Kipper et al. 2004). This finding reflects the possibility that selective addition and attrition of song types might lead to an increased similarity of song type repertoires which might explain the large repertoire overlap observed between older males within our study population (on average approx. 55%, P. Sprau and R. Mundry pers. comm.) as compared to repertoire overlap within other nightingale populations (Hultsch and Todt 1981). Laboratory studies corroborate the assumption that nightingales can in fact add song types to their repertoires that they heard in their first season (Todt and Geberzahn 2003). They also 'activated' song types they had heard during their early sensitive phase of auditory song learning but which they did not sing until they were re-exposed to those songs after crystallizing of their song (Geberzahn et al. 2002).

Such an increased similarity that has been reported for other species, too, is apparently advantageous in different behavioural contexts such as territory tenure, vocal and physical interactions, survival and reproductive success (reviewed in Handley and Nelson 2005).

In addition we found no correlations between repertoire size in the first breeding season and increase (neither net gain nor relative increase). This result suggests that there is no relationship between increase and quality. Interestingly however, we found that males with larger repertoires in their first season subsequently added more song types to their repertoire. This finding, together with the correlation of first and second season repertoire sizes, suggests that higher quality males (with larger repertoires) are better able to adjust their repertoires to those of the locally present males than lower quality males (with smaller repertoires).

The frequencies with which birds sang their song types did not correlate between the first and the second season in five of six individuals. In contrast, song type frequencies in older birds are positively correlated between seasons (Kipper et al. 2004). Interestingly, though, subjects sang those song types more frequently in their first season that they retained in their second season's repertoire. Possibly, this reflects an adjustment of repertoires to the locally prevalent song types already beginning in the first season.

Our current results fill the gap between previous findings (Kiefer et al. 2006, Kipper et al. 2004, 2006), by showing that individual nightingales both increase and remodel their repertoire much more dramatically between their first and second breeding season than later on. We therefore propose the hypothesis that nightingales adjust their repertoires between the first and the second breeding season based on the songs sung in their population. Based on this hypothesis, the exact use and function of shared song types should be addressed in playback studies.

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