LONG-TERM PERSISTENCE OF SONG PERFORMANCE RULES IN NIGHTINGALES (LUSCINIA MEGARHYNCHOS): A LONGITUDINAL FIELD STUDY ON REPERTOIRE SIZE AND COMPOSITION

by

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(Acc. 7-I-2004)

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Summary

Common nightingales (*Luscinia megarhynchos*) are among those bird species that possess an extremely large repertoire and perform it in a versatile singing style. Thereby, repertoire size, composition, and performance differs considerably among individuals. In this longitudinal field study, we investigated the long-term stability of these differences in the song characteristics of free-ranging nightingales. We determined the repertoire characteristics for nine adult male individuals in two successive years (three of these individuals were investigated over the course of three years) and compared these to similar measurements obtained from comparisons of song samples of different birds. Comparisons revealed remarkable differences among males, but we did not find systematic differences in the song performance of birds in successive years. Instead, song characteristics were remarkably stable within successive years. The long-term persistence of individual song characteristics suggests that they are not related to dynamically changing individual attributes, but may reflect long-term storage of information during song acquisition as juveniles. In addition, we found that the repertoire performance of adult nightingales allows fine-tuned vocal interactions among several neighbouring males.

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Introduction

The study of song repertoires has a long history, and several hypotheses have been put forward to explain their proximate function and their adaptive value (review in Catchpole & Slater, 1995). Such explanations range from the avoidance of habituation (Hartshorne, 1956) or exhaustion (Lambrechts & Dhondt, 1988) to the mimicking of several conspecifics (Krebs, 1977) or implications in aspects of inter- or intra-sexual selection. Here, females could prefer males with large repertoires (Searcy, 1992), as was shown for sedge warblers (*Acrocephalus schoenobaenus*, Buchanan & Catchpole, 1997) and pied flycatchers (*Ficedula hypoleuca*, Lampe & Saetre, 1995). On the other hand, repertoire sizes seem to play a role in male-male encounters where large repertoires may allow a singing individual to specifically address several different neighbours (review in Todt & Naguib, 2000). This has been documented *e.g.* for Eurasian blackbirds (*Turdus merula*, Wolffgramm & Todt, 1982), common nightingales (*Luscinia megarhynchos*, Hultsch & Todt, 1981), and song sparrows (*Melospiza melodia*, Beecher *et al*., 2000). With regard to repertoire sizes in successive years, there is some indirect evidence that the acquisition of a large repertoire is costly, since in some species repertoires increase with age (*e.g.* canary, *Serinus canaria*, Nottebohm & Nottebohm, 1978; European starling, *Sturnus vulgaris*, Mountjoy & Lemon, 1995), and females prefer to mate with males that possess larger repertoires (Searcy, 1992).

Besides such functional aspects, the proximate aspects of song repertoires were examined, for example, concerning the rules of repertoire development and performance and the neurobiology of song delivery and the mechanisms of its sensorimotor control (Tchernichovski *et al*., 2001; Brainard & Doupe, 2002). Since the performance of a repertoire can be taken as a reflection of information stored in a bird's memory, it is possible to use non-invasive approaches in addressing such mechanisms (Todt & Hultsch, 1996). The feasibility of this approach has been verified by the success of many such inquiries into the processes of song learning. These uncovered *e.g.* factors influencing the memorisation of song material or promote its development and its crystallisation (review in Hultsch & Todt, in press).

Aside from a few exceptions in which birds learn single songs only, most species acquire repertoires of several song patterns. However, the size of such repertoires differs a lot across oscines species (review in Hailman & Ficken,

1996). Differences in repertoire size are often linked to specific modes of song delivery. Species with small repertoires usually repeat a given type of song several times before they switch to a new one (*e.g.* great tit, *Parus major*, Krebs, 1976; chaffinch, *Fringilla coelebs*, Slater, 1983), whereas birds with large repertoires preferentially sing in a versatile manner with immediate variety. This singing style, in which birds usually switch to a new song type after each song occurs, for example, in nightingales (Hultsch & Todt, 1981), song thrushes (*Turdus philomelos*, Ince & Slater, 1985), and in northern mockingbirds (*Mimus polyglottus*, Derrickson, 1988). Within versatile singing, songs are rarely delivered at random (review in Catchpole & Slater, 1995). Instead, for a number of species it was shown that the succession of songs or elements within a song bout follows sequential rules (*e.g.* European starlings, *Sturnus vulgaris*, Eens *et al.*, 1989; sedge warblers, *Arocephalus schoenobaenus*, Catchpole, 1976; Eurasian blackbirds, *Turdus merula*, Todt, 1975). Studies on the song acquisition of hand-reared nightingales showed that males not only learn song types, they also learn particular rules of song type sequencing, too (review in Hultsch *et al.*, 1999). Therefore, inquiries into the performance rules of song type repertoires allow to investigate additional measures of variability or stability in the song performance of a bird.

The majority of research on repertoire development has been conducted under laboratory conditions. It remains an important issue to supplement the available results with findings of studies carried out in the field (Beecher, 1996). The appropriate design of such a study was discussed recently by Gil & Slater (2002; see also Forstmeier, 2002). They suggested a comparison of cross-sectional and longitudinal approaches. In this paper, we are presenting a longitudinal field study on adult nightingales. The common nightingale is renowned for its large song type repertoire, in which adult males may orchestrate about two hundred different types of songs. The use of such large repertoires seems to be related to the ability of individuals not only to learn during their natal summer, but also to memorise and imitate new songs later in life (*e.g.* Chaiken *et al.*, 1993; Todt & Geberzahn, 2003). We determined the repertoire composition and performance of these birds and examined the long-term persistence of these traits for the first time. Laboratory studies have shown that nightingales possess a number of mechanisms to modify their repertoire composition and singing style later in life. For example, during a late phase of vocal learning, birds are able to learn new song types and include them in their repertoire almost immediately (Todt & Geberzahn,

2003). In addition, a study of Geberzahn & Hultsch (2003) indicated that nightingales store more song types in their sensory phase than they spontaneously recall from memory as adults. With regard to these mechanisms and possible functions of larger repertoires for the attraction of females or for interactions among males, we hypothesised that the repertoire sizes of free-living birds would increase from year to year and, as a consequence of repeated interaction and learning, we also expected an increase in repertoire sharing between the birds of a given population. At the same time, we were curious about whether and how the rules of individual repertoire performance would change over successive years.

Methods

Animals and study site

The study was conducted in April and May of 2000 to 2003 in Treptower Park, a municipal park in the city of Berlin, Germany. The park (size: approx. 0.9 km^2) is composed of habitats including dense bushes, clusters of broad-leafed trees and regularly cut grasslands, ponds and rivers (Fig. 1). The population density of territorial male nightingales in the park varied between years (2000: 24; 2001: 31; 2002: 27; 2003: 26 individuals). After returning from winter quarters in Africa, males tend to inhabit the same areas, often even the same territory as in the previous year (Glutz von Blotzheim, 1988). They use mainly one particular song-post for nocturnal singing and rarely switch song-posts during long singing bouts (Hultsch & Todt, 1981). In 2001, we began colour-ringing adult males in the park. Males were captured using mist nets in the territory in which they had been observed for at least three days following their arrival in the area. We captured birds with permission of the Senatsverwaltung für Stadtentwicklung and on behalf of the Vogelwarte Radolfzell (Beringungszentrale an der Max-Planck-Forschungsstelle für Ornithologie). No bird deserted its territory after capture.

Seven of 17 males ringed in 2001 returned to the park in 2002. In 2003, 4 birds returned for a third year and five for a second year. For seven of these ringed males (aged 2 years or older), we obtained recordings of nocturnal singing bouts during two successive years and were therefore able to compare repertoire characteristics in these years. In addition, we investigated the repertoire composition of several non-ringed birds recorded in 2000 and 2001. Here, two males occupied the same territory in both years and were recognisable by specific characteristics of their repertoire. They showed the same similarities in repertoire composition as birds identified by coloured rings, which led us to the conclusion that these were the same individuals. Furthermore, for three birds, we were able to make third-year recordings and accordingly extended our analyses.

Recordings and determination of song type repertoires

We recorded nocturnal singing bouts (at least 90 min without interruptions longer than 20 s) with a Sennheiser ME 80/K3U or ME66/K6 directional microphone connected to a Sony TCD 5 tape recorder or a Sony TCD D-100 DAT recorder. At the time of recording, the
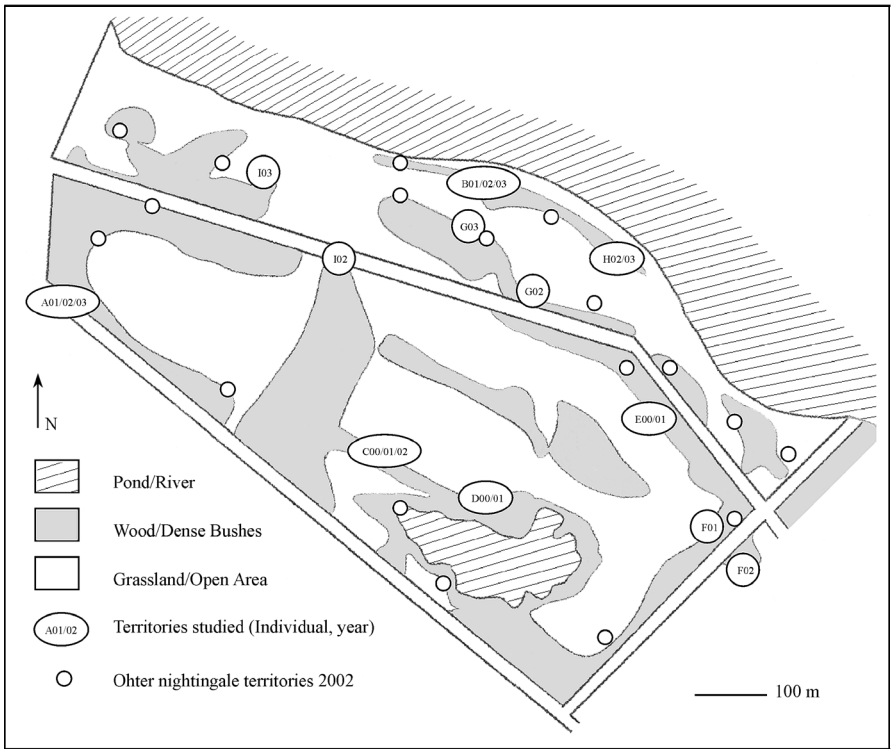
Fig. 1. Map of the study site. Indicated are territories of individuals studied. Additionally, all territories occupied by males in 2002 are marked in order to give a measure of territory density.

exact pairing status of males was unknown, but all individuals continued nocturnal singing. According to a study of Amrhein *et al.* (2002), this indicated an unpaired status or mated status at the onset of breeding.

For data analysis we used recordings of at least 531 consecutive songs per male (Table 1). Depending on song rate, this corresponded to a singing bout of approximately one hour duration. Analysing such large numbers of songs resulted in cumulative repertoire curves that converged saturation.

First, we determined the song type repertoire for each bird and each year by applying the criteria suggested in Hultsch & Todt (1981). Thereby, we characterised songs as belonging to the same song type when they differed in not more than three of approximately ten element types in the first two sections of the song and included the same repetitive sections (see Fig. 2 for illustration). Through application of these definitions, we were able to assign each song of a bird to a song type already performed or established a new type (with few exceptions, see Table 1). In a next step, we compared the song type repertoires in successive years, applying the same definitions of categorisation. Additionally, we conducted an inter-individual comparison by investigating song type sharing between different birds in the same year.

TABLE 1. *Details of song samples analysed*

Individual	Year	Length of analysed song sequence[1]	Number of songs not assigned to a song type[2]	Repertoire size
A	2001	553	0	165
	2002	567	2	159
	2003	*593*	*11*	*167*
B	2001	564	4	189
	2002	541	1	207
	2003	*598*	*1*	*206*
C	*2000*	*537*	*5*	*197*
	2001	531	7	200
	2002	549	3	195
D	2001	556	1	166
	2002	539	1	170
E	2000	537	3	190
	2001	571	2	195
F	2000	812	27	231
	2001	908	4	227
G	2002	545	0	151
	2003	559	1	154
H	2002	596	2	225
	2003	573	3	200
I	2002	550	6	156
	2003	600	3	160

Samples that were used only for a three-year-comparison are given in italics.

[1] For most of the analyses we used only a subset of this sequence, see methods for details.

[2] In most cases, these were interrupted songs.

Comparison of song samples and statistical analyses

To quantify similarities between two recordings from the same subject in different years, or from different subjects recorded in the same year, we applied the following measurements. First, we measured repertoire sharing between two sequences using the DICE-coefficient C_D (Norušis, 1994) with $C_D = 2 *$ number of shared song types / (repertoire size in one sample + repertoire size in the other sample). Secondly, we determined for each song type its frequency in each of both samples to be compared and tested whether frequencies obtained from the two samples correlated with one another. We repeated this analysis twice, once including all song types, and once including only song types that occurred at least once in either of the two samples. In addition, we tested whether the frequency of occurrence of a
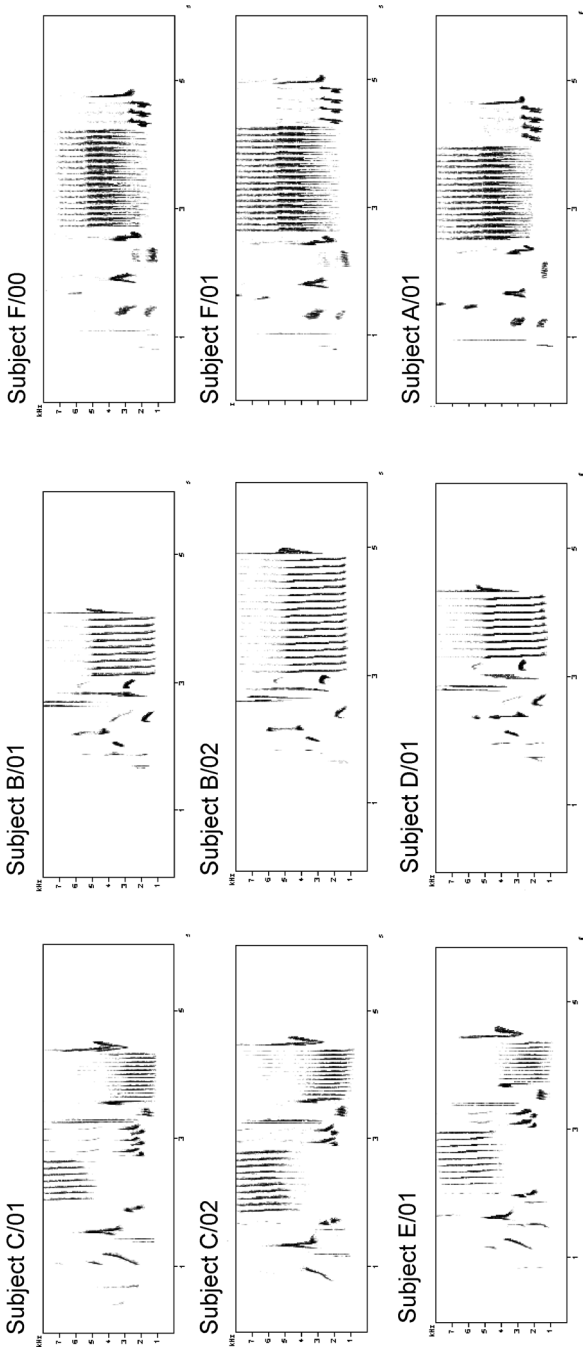
Fig. 2. Three song types in nightingales. The two upper spectrograms of a column show songs performed by the same individual in successive years, the lower row shows a song of the same type performed by another bird. All samples were chosen at random and not with regard to highest similarity.

given song type in a given bird in one year was related to its presence or absence in the other year. We did this by applying Mann-Whitney U-tests with presence/absence in one year as the predictor variable and frequency of occurrence in the other year as the response variable. Since both years recordings were used once as predictor and once as response variable we applied two tests per subject. Finally, we compared first order transition rates between song types between pairs of sequences using matrix-correlation and tested the significance of the derived correlation coefficient using the Mantel-test (Sokal & Rohlf, 1995). Only those song types which occurred in either of the two samples to be compared were included in this analysis.

To assess the degree of stability of an individual's song characteristics from one year to the next, we first compared corresponding repertoire sizes. To control for differences between numbers of songs in the different recordings, we determined each subject's repertoire size from a sequence with a standardised number of songs equalling the shortest sequence analysed (1st year of subject C: 524 consecutive complete songs, songs that were not assigned to a song type were left out, see Table 1). In addition, we estimated the repertoire size using a jack-knife procedure as suggested by Garamszegi *et al*. (2002) and applied it to the sequences. This measure gives an estimate of the 'real' repertoire size of a bird on the base of the frequency of occurrence of song types within a given sample. Although this procedure is best suited to a random song type delivery, we nevertheless decided to use it as later in a song bout, new song types did not occur in associations, but rather singly among other, repeatedly performed song types (see repertoire curves).

Furthermore, we measured the degree of order within sequences of song types. We did this by determining how often each pair of song types in a given sequence occurred with a specific number of songs in between them, regardless of the order of their occurrence (a $\geqslant$ b or b $\geqslant$ a). Thus we obtained one asymmetrical matrix per distance between song types and sequence analysed, indicating corresponding frequencies for each pair of song types, separately. We then applied the Shannon-Weaver measure of entropy ('H') as a means to describe the degree of heterogeneity of entries in the matrix (Chatfield & Lemon, 1970). If certain song types preferably occurred at specific distances to certain other song types then H would be relatively small. On the other hand, if song types did not exhibit such preferred distances to certain other song types, then H would be larger. To test the statistical significance of a given value of H we used a permutation procedure. As an overall measure of the degree of order in a given sequence we then used the largest distance between songs that revealed a significant value of H and for that at the same time each smaller distance revealed a significant H. The resulting value (here termed 'window size') can be regarded as an average time window (indicated as a number of songs) within which the occurrence of song types is not independent.

To test whether repertoire turnovers between years could be due to insufficient sample sizes we used a permutation test. For this test we randomised the songs actually sung between the two samples of a subject. We used the number of song types which occurred at least twice in the total sample of songs and which were present in only one of the respective samples as the test variable.

With the exception of the Mantel-test, we applied non-parametric tests based on ranked data throughout the study. Since several measures (*e.g.* song type frequencies) included a considerable amount of tied ranks we generally derived p-values corresponding to Mann-Whitney U-tests and Spearman's rank correlation coefficients from a permutation procedure (termed Monte-Carlo procedure in SPSS) rather than from critical values tabulated in books.

We used Wilcoxon-tests to check whether properties of song samples systematically changed from one year to the next and non-parametric correlations to test for the stability of sequence properties within subjects. We calculated mantel-tests, Spearman's rank correlation coefficients as well as the Shannon-Weaver measures of entropy and corresponding p-values using self written software. All other tests were calculated using SPSS 11.0.1 for Win98. In the case of small samples, we applied exact tests. In all other cases were applied approximate tests using 10,000 permutations (Mundry & Fischer, 1998) or 1,000 permutations in the case of the Mantel-test and the permutation test of repertoire turnover. To adjust the error-level for multiple testing of repertoire turnover we combined the derived p-values using Fisher's omnibus test (Haccou & Meelis, 1994). The determination of the window size was based on 1,000 permutations. We indicate two-tailed p-values throughout the results.

Results

Comparison of song samples from same and different subjects

In general, any two song samples recorded from the same subject in two successive years exhibited a larger overall similarity than any pair of samples recorded from different subjects recorded in the same year. For instance, the proportion of shared song types (DICE-coefficients) between two recordings of the same subject obtained from different years was always larger than 0.83 and thus clearly larger than corresponding figures obtained from recordings of different subjects made in the same year (maximum: 0.66; Fig. 3a). Also with regard to the frequencies with which subjects sang different song types, we found that similarities between samples from the same subject were always larger than similarities between samples from two different subjects. This was shown in regard to all song types (Fig. 3b) as well as regarding only song types present in both samples (Fig. 3c). In addition to these findings for repertoire composition, regarding the characteristics of repertoire performance, a general tendency towards larger correspondences between any two samples recorded from the same subject than between any two samples recorded from different subjects was found (Fig. 3d). In a few cases, the succession of song types sung by the same subject in two consecutive years exhibited remarkable overall similarity (Fig. 4a). However, this was not the rule in all subjects analysed (Fig. 4b), and, in fact, in some instances song sequences of different subjects showed clear correspondences as well (Fig. 4c).
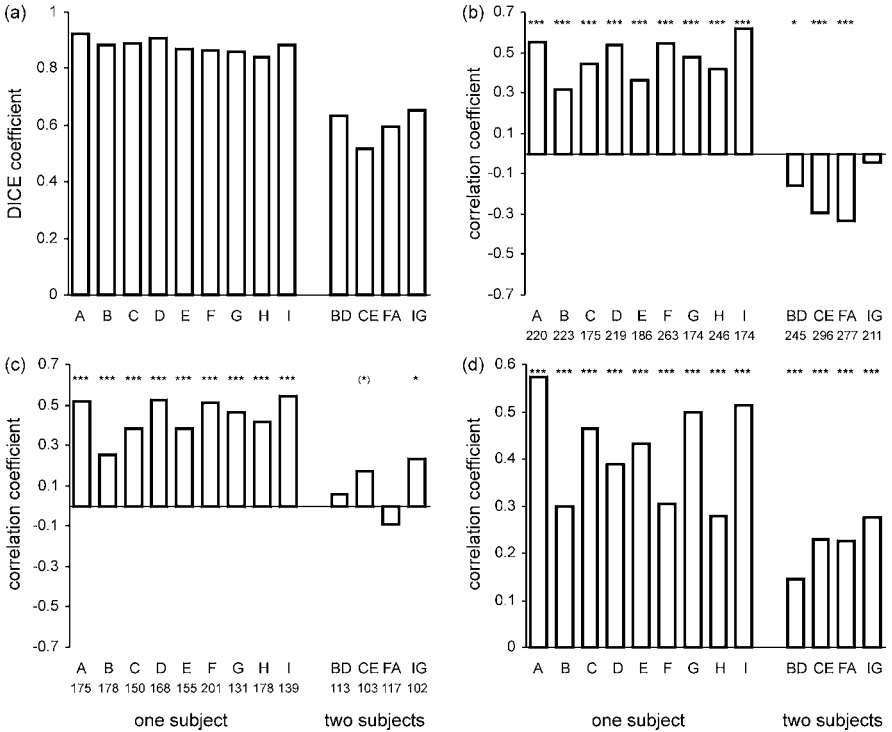
Fig. 3. Similarities between song samples obtained from the same subjects in two succes-sive years (left nine bars), or from different subjects in the same year (right four bars; pairings were selected at random). Shown are (a) DICE-coefficients of repertoire sharing (large coef-ficients indicate a large proportion of shared song types between two recordings), (b) Spear-man's correlation coefficients between frequencies of song types, for all song types, as well as (c) only for song types present in both samples to be compared, and (d) Pearson's cor-relation coefficients between first order transition matrices for song types. Sample sizes for (b) and (c) are indicated below the bars and correspond to the total number of song types (b), or to the number of shared song types (c) in the two samples. The number of transition rates analysed in (d) equals the square of the corresponding number of shared song types (indicated below c). ***: $p < 0.001$; *: $p < 0.05$; (*): $p < 0.1$; based on Spearman's rank correlation coefficient (b, c) or the Manteltest (d). In each of the four measures similarities between sequences of the same subject were significantly larger than similarities between se-quences from different subjects (Mann-Whitney U-tests, all $N_{\text{same subjects, different years}} = 9$, all $N_{\text{different subjects, same year}} = 4$, all $U = 0$, all $p = 0.003$).

Individual stability of song samples

With regard to the general degree of order within song sequences and re-garding repertoire sizes, we found that the properties of same subjects dif-
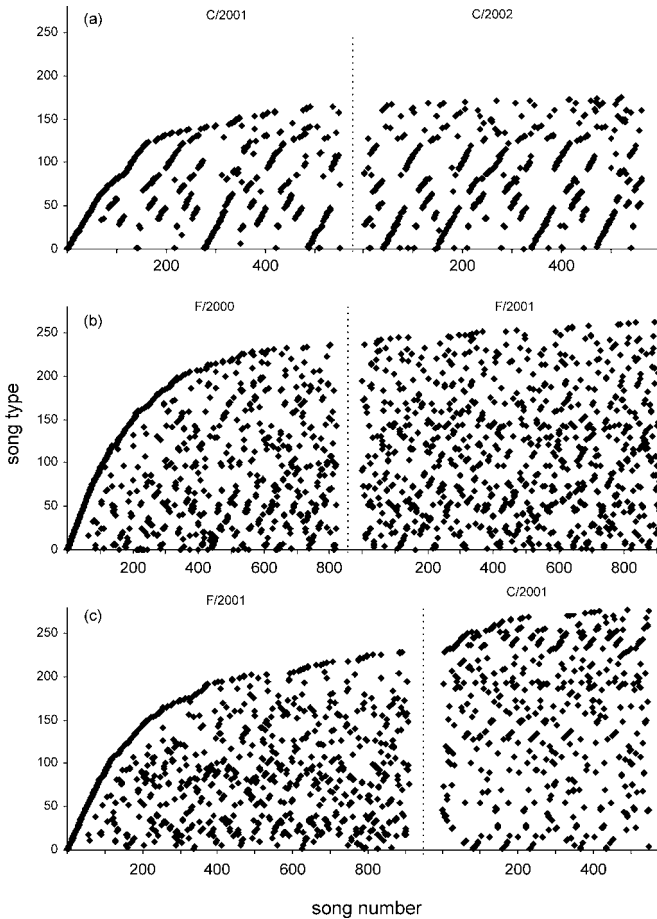
Fig. 4. Sequences of songs of the same subject recorded in two successive years (a: subject C; b: subject F) or of two different subjects recorded in the same year (c: subjects F and C). Each song is denoted by a dot, songs of the same type are depicted at the same distance from the x-axis. Dotted lines separate different recordings. Note the large similarity between the two sequences of subject C (a), the much weaker correspondence of the two sequences of subject F (b), and that several song types seemed to occur sequentially associated in subject F as well as in subject C (c).

fered only slightly between years, in contrast to differences between different subjects within one year. In fact, the larger the general degree of order in a sequence recorded for a given bird in one year, the larger it was in the other year, as well (Spearman's rho: $r_S = 0.89$; $N = 9$; $p = 0.002$; Fig. 5a). Corresponding results concerning repertoire sizes showed similar tendencies:
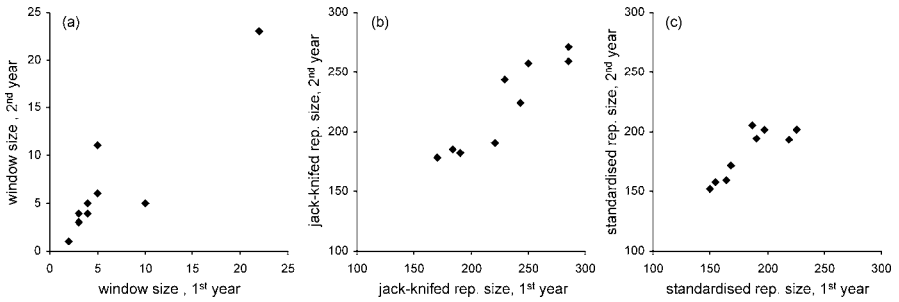
Fig. 5. Relations between characteristics of song samples from the same subjects in two successive years. Indicated are (a) average time windows (numbers of songs) within which the occurrence of song types was not independent, (b) song type repertoire sizes determined from samples using a jack-knife method, or (c) with standardised numbers of songs. Measures indicated in (a) an increase with the general degree of order in a song type sequence. Note also that the particularly large figures in (a) were obtained from subject C depicted in Fig. 4a.

jack-knifed estimates of repertoire sizes derived for different recordings of the same subject clearly correlated with one another ($r_S = 0.96$; $N = 9$; $p < 0.001$; Fig. 5b) as did repertoire sizes derived from samples of a standardised number of songs ($r_S = 0.76$; $N = 9$; $p = 0.02$; Fig. 5c).

Differences between song samples

Despite the large overall similarity between repertoires determined for the same respective subject in two successive years, in each recording of each subject we were able to find some song types that were performed in only one of the two years. In fact, the proportion of song types found in one year but not in the other ranged from 6% (second year recording of bird A) to 21% (first year recording of bird H). The frequency of the use of song types showed a relationship to their persistence over the years: individuals performed song types that were present in both years clearly more often than those present in only one of two years (18 Mann-Whitney U-tests, all $N_{both\ years} \geqslant 131$, all $N_{only\ one\ year} \geqslant 10$, all $U \geqslant 353$, all $p \leqslant 0.03$). This apparent repertoire turnover between two recordings of a subject might, however, not reflect the actual appearance of 'new' and deletion of 'old' song types but may rather arise due to the fact that a bird did not perform all of its stored song types within the analysed recordings. To rule out this possibility, we conducted a permutation test. It indicated significance ($p < 0.05$) in only one subject (G) suggesting that this bird indeed could have added or deleted

song types from its repertoire. However, this finding could have also arisen from multiple testing, and, in fact, the combined p-value for all subjects equalled 0.23 suggesting that songs occurring in one year but lacking in the other reflected actual performance decisions of the birds rather than a repertoire turnover.

Finally, we tested whether properties of sequences systematically changed from one recording to the next. We were unable to find any hints that such systematic changes did exist (Wilcoxon tests; standardised repertoire size: $T^+ = 22.5$; $N = 9$; $p = 1$; jack-knifed repertoire size: $T^+ = 34$; $N = 9$; $p = 0.20$; window size: $T^+ = 19$; $N = 7$ (2 ties); $p = 0.52$).

Long-term stability of individual song characteristics

For three birds, we analysed song sequences from three successive years (individuals A, B, C, see Fig. 1 and Table 1). For these analyses, we conducted all comparisons of repertoire characteristics as described above additionally for the second and third, and first and third season. In all cases, the results were in agreement with the results of our two-year-comparisons. We did not find differences in the repertoire size, repertoire composition, or repertoire performance among the three subjects. Figure 6 illustrates the proportion of songs occurring in three, two, or only one of three successive years. For song types that were performed in only two of three years, it is interesting to note that these were not only song types performed in two successive years. Instead, we found some song types that occurred in the first and third, but not in the second year for all birds. In addition, as can be seen in Figure 6b, song types that occurred in all three years were performed more often than songs which were recorded in only one of the years.

Discussion

Contrary to our predictions, repertoire size, composition, and song performance rules of the nightingales studied did not show any systematic change across successive years. Instead, these traits remained remarkably stable over the years. In addition, song type repertoires, frequencies of song types and preferred transitions between them indicated individual-specific differences and allowed for a reliable identification of subjects. Nevertheless, some correspondences in repertoire composition and song type sequences
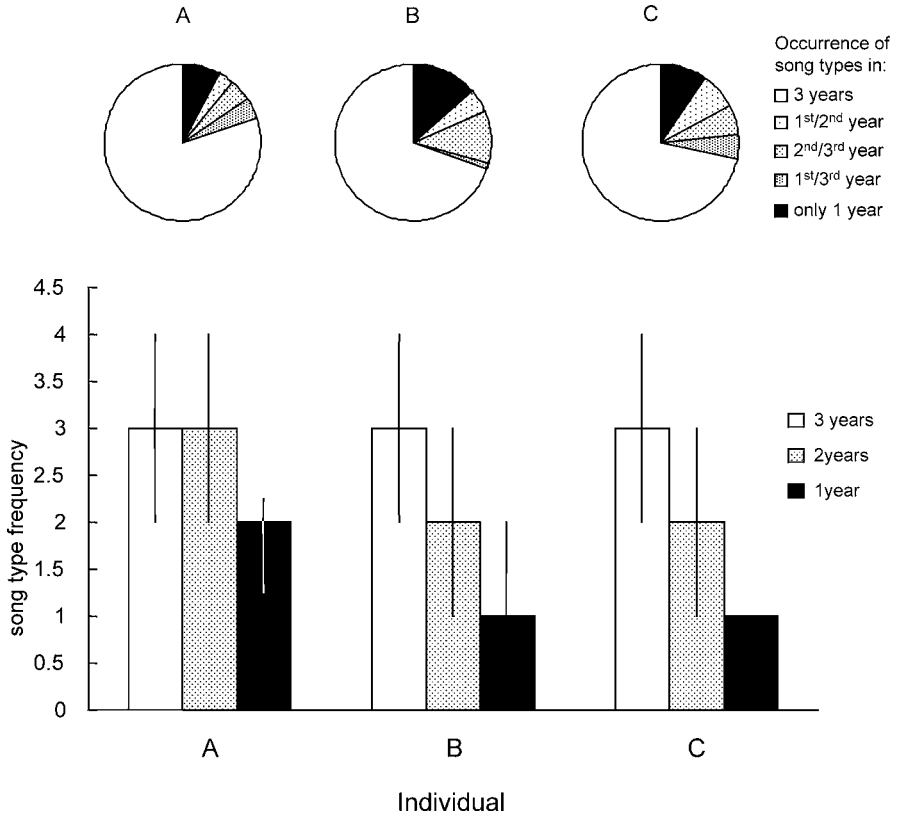
Fig. 6.   Top: proportion of song types that occurred in all, two, or only one of three years. Bottom: frequency of occurrence of song types that occurred in all, two, or only one of three years. (For songs that occurred in two or three years, the occurrence frequency of a song type was determined as the mean of the respective frequencies in two or three years).

between different individuals were evident as well. Inter-individual comparisons showed that coefficients of repertoire sharing between different birds in a given year were lower than coefficients for same birds in successive years. These results invite a discussion of age-related effects on song repertoires and on the use of large song type repertoires.

Age-related effects

As stated in our introduction, we expected an increase in the repertoire sizes of wild nightingales from year to year and also that repertoire sharing between birds of a population would increase. This was suggested by results of

laboratory studies (Todt & Hultsch, 1998; Geberzahn & Hultsch, 2003) and by field studies of other bird species (*e.g.* indigo bunting, *Passerina cyanea*, Payne, 1981). In willow warblers (*Phylloscopus trochilus*), several repertoire characteristics such as repertoire size and element rate change with age (Gil *et al.*, 2001). Here, changes between the birds' first and second year of age were explained by delayed maturation. However, in our study the situation was different as all subjects were older than one year by the first recording. This age composition could explain why our expectations were not confirmed by our results. One would need to compare repertoire characteristics of yearlings and adult birds in order to investigate whether the repertoire characteristics of an individual are already fully developed in the bird's first year singing.

On the other hand, our results agree with findings on northern mockingbirds (*Mimus polyglottus*, Derrickson 1988), pied flycatchers (*Ficedula hypoleuca*, Espmark & Lampe, 1993), and song sparrows (*Melospiza melodia*, Nordby *et al.*, 2002). In these species, no differences in song characteristics were found in successive years, but large individual differences occurred between males. Given the striking differences in the repertoire sizes and styles of song type delivery in these species, we conclude that the persistence of repertoire characteristics cannot be interpreted as a direct consequence of a large song repertoire. In these song bird species, the repertoire size and performance obviously does not reflect age-related qualities of a male.

The use of large song type repertoires

There are many hypotheses on the factors that promoted the evolution of song repertoires (review in Catchpole & Slater, 1995). The most important ones concern aspects of inter-sexual selection (Slater, 2003). However, it has yet to be confirmed that female choice played a significant role in the development the repertoire characteristics in nightingales. We have shown that several basic properties of song samples recorded from same individuals remained consistent over successive years. Since these properties, although certainly adaptive, did not reveal any systematic changes over time, we conclude that there was no functional force which had continuously shaped them into a particular direction over the years. Therefore, the results of our study suggest that repertoire size, composition, and song performance rules are not related to rapidly changing individual attributes, such as nutritional status or status within the breeding cycle. Instead, given the large differences

between individuals, these repertoire characteristics may reflect the bird's state during the phase of song acquisition, *i.e.* at the time of sensory learning during the first month of life. For great reed warblers (*Acrocephalus arundinaceus*, Nowicki *et al.*, 2000) and European starlings (*Sturnus vulgaris*, Buchanan *et al.*, 2003) it was shown that the body condition at the phase of song acquisition might determine the individual characteristics of song performance rules. A study on song sparrows (*Melospiza melodia*, Nowicki *et al.*, 2002a, b) has additionally shown that females discriminate according to learning abilities of males. This provides further evidence that song learning abilities might function as an indicator of a male's quality.

It is important to remember that song characteristics not investigated in our study might reflect other aspects of a male's quality and play a crucial role in attracting females. It was shown, for example, that (at least male) nightingales treat songs with a specific quality, so called 'whistle songs', as a song category with a specific signal value (Naguib *et al.*, 2002).

In species such as nightingales, which have a versatile singing style, we often observe elaborated vocal encounters among males involving pattern-specific and time-specific responses (Todt, 1981; Naguib, 1999), as well as adjustment of body orientation (Brumm & Todt, 2003) and song amplitude (Brumm & Todt, in press). Such repeated interactions among neighbouring males might facilitate the development and use of large repertoires as these would allow more specifically addressed vocal encounters. Repertoire sharing allows engagement in pattern specific interactions, *e.g.* matched countersinging. Additionally, large repertoires should be structured by certain rules of song performance because this facilitates song retrieval from memory and thus allows to also engage in time specific interactions (Hultsch & Todt, in press). Our findings showed that all these requirements were fulfilled by the studied nightingales. Therefore, we conclude that males may benefit from repertoires large enough to specifically address several different neighbours (Todt, 1981; Beecher *et al.*, 2000). However, this does not necessarily mean that close neighbours should share most song types. Hultsch & Todt (1981) found that neighbours in intermediate distances shared a higher proportion of songs than close or distant neighbours. Again, a long-term study on the development of repertoire similarities within a larger population of birds could help to further illuminate the role of male-male interactions in the development of repertoire characteristics.

Referring to research on neurobiological substrates and processes underlying song acquisition and storage (review in White, 2001; Nottebohm, 2002), we would expect a considerable turn-over in repertoire composition between successive years. Instead, the relative stability in repertoire composition over two or more years suggest that nightingales posses a large repertoire of stored song types, but do not perform all types within a given singing bout. This result is in accordance with studies on hand-reared nightingales, indicating that the birds stored more song types than they actually perform in a given season (Geberzahn & Hultsch, 2003). In order to understand how nightingales were able to achieve the documented persistence of song properties and decide which song types to sing, further studies are needed. These could examine, for example, whether the birds sing in their winter-quarter and if they consolidate their repertoires thereby.

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