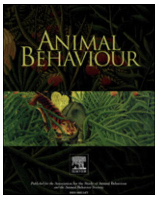
Animal Behaviour 80 (2010) 427–434

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Song type sharing in common nightingales, *Luscinia megarhynchos*, and its implications for cultural evolution

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ARTICLE INFO

Article history:
Received 16 June 2009
Initial acceptance 30 July 2009
Final acceptance 17 May 2010
Available online 20 July 2010
MS. number: 09-00395R

Keywords:
birdsong
common nightingale
communication
cultural evolution
Luscinia megarhynchos
repertoire composition
song sharing

The sharing of song types between males of the same local population is a common phenomenon in some songbird species. One presumed advantage of such sharing is that it enables 'song matching' (i.e. responding to an interactant with the song he just sang or another song of the interactant's repertoire). Song sharing probably arises through song learning, whereby males of some species prefer acquiring songs shared in the local population. However, such a preference may lead to uniformity of repertoires, devaluating the signal value of shared songs. Here we investigated repertoire composition in a local population of nightingales. More precisely, we analysed the number of song types shared by a given number of males and compared the finding with different simulated models of song acquisition. We found that proportions of both (songs shared by many males as well as songs sung by a single male only) were clearly more common than expected. We also simulated the cultural evolution of the population's repertoire. The results of these simulations supported our conclusion from the simulation of song acquisition that unshared songs arise through invention of novel song types or modification of existing ones, although we cannot rule out that unshared songs also appear through immigration of males. Our findings suggest that nightingales have a preference to acquire both shared song types, which enable matching the songs of opponents, and unshared or 'invented' new song types, which may help to avoid being matched by opponents.

In several songbird species, individual males possess a repertoire of several distinct song types, and males settling in the same neighbourhood often show some overlap in the composition of their individual repertoires (reviewed in Catchpole & Slater 2008). One hypothesis about the existence of repertoire sharing is that it allows for more differentiated forms of vocal interactions, such as song matching. So far, two forms of matching have been described: 'song type matching' in which a male sings the same song type that its opponent just sang (e.g. Todt 1971; Krebs et al. 1981), and 'repertoire matching' in which a male sings a song other than the one its opponent just sang but that is part of the opponent's repertoire (Beecher et al. 1996). Both are considered to be repelling signals, with the former indicating the more agonistic motivation (Beecher et al. 1996; Burt et al. 2001). Furthermore, by matching the song of an interactant, males can direct their agonistic intention towards a certain opponent, and this may be important for the successful acquisition and maintenance of a territory (Beecher et al. 2000). An until now rarely considered aspect of matching is its passive component, that is, singing unshared songs. The use of unshared songs may be advantageous to avoid being matched or to avoid agonistic signalling towards an interactant (i.e. to avoid repertoire matching). For instance, Beecher & Campbell (2005) found evidence that, compared with singing shared songs, singing unshared songs is the 'more effective de-escalation signal' in the song of song sparrows, *Melospiza melodia*. Singing unshared songs, however, may also enable birds to express individuality and thus be advantageous for territory maintenance (Nordby et al. 2007).

In terms of song development, song sharing is likely to be the result of song learning, which is considered to occur in all oscine songbird species (Kroodsma & Baylis 1982). Sharing song types, however, may not exclusively be the consequence of different birds accidentally acquiring the same song type. Instead, young birds of some species seem to have a preference for incorporating songs in their repertoire that are shared by more males of the local population (Beecher et al. 1994; Nordby et al. 2000; Kiefer et al. 2010). However, this song acquisition strategy may lead to considerable uniformity in repertoires, making the singing of unshared songs inevitable, when only few unshared songs remain available for two interacting males. Hence, one could expect the acquisition process to be more complex and that birds, besides preferentially acquiring

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doi:10.1016/j.anbehav.2010.05.028

songs shared by many males, also acquire songs being sung by only few males or songs that are unshared. Such unshared songs may simply be the consequence of copying mistakes. However, individually distinctive songs may also be the consequence of modifications (Nordby et al. 2007) or recombinations (Hultsch et al. 1998) of learned shared songs.

In this study we analysed the repertoire composition of male nightingales from a local population. More precisely we determined the number of song types shared by a given number of males. Fully mature nightingales possess extraordinarily large song type repertoires of approximately 180 song types (Hultsch 1980; Kipper et al. 2004, 2006; Kiefer et al. 2006), which can overlap considerably between males of a neighbourhood (Hultsch & Todt 1981). In addition to this empirical study we conducted a simulation study investigating the cultural evolution of song sharing under different acquisition models and for different numbers of tutors available. Particularly, we investigated how song sharing in a population of nightingales would develop when males acquire their songs from a pool of available songs with or without a probability proportionate to the number of males sharing a song.

METHODS

Study Subjects

We analysed nocturnal song of 12 birds recorded in 2004 in the Treptower Park, an urban park in the centre of Berlin, Germany. Nine of the subjects were recorded before 29 April, and hence presumably before or during pairing. The other three males (recorded on 4, 11 and 25 May) were presumably unpaired, as they were still singing nocturnally (Amrhein et al. 2002). Recordings were made as part of an ongoing long-term study on communication and ecology of nightingales (Kipper et al. 2004, 2006; Kiefer et al. 2006, 2009, 2010; for details of the study site see Kipper et al. 2004). Six of the males included in the study were colour banded in one of the previous years and were hence known as being fully mature (i.e. in at least their third calendar year). The other six males presumably newly entered the study site in 2004 and were identified as fully mature by the complete absence of any features suggesting them to be in their second calendar year (Svensson 1992; Kiefer et al. 2006; Mundry & Sommer 2007). The territories of the males investigated were scattered throughout the park, with each male included having at least one other male and usually several others within earshot (Fig. 1).

Recording and Analysis of Songs

We analysed 533 songs from each male (smallest sample available from any of the males). Such a sample size usually allows for the identification of the great majority of an individual's repertoire (Kipper et al. 2004, 2006; Kiefer et al. 2006). All analysed songs of a certain male were from a single recording and usually sung consecutively, with the occasional exception of short gaps in the sequence caused by interrupted songs that we could not identify. For deriving the combined repertoire of the studied males, we built up a catalogue of the song types found and visually compared each song of each male with all songs of the catalogue. Song types of nightingales are rather fixed with regard to element combination and sequence (also across different males) and hence easily and unambiguously recognized (Hultsch 1980; Kipper et al. 2004, 2006; Fig. 2). We defined songs belonging to the same song type when the repetitive parts of the songs were identical, irrespective of the number of repetitions of the elements or syllables. In a few cases males differed only in the initial nonrepetitive parts of songs. If these initial nonrepetitive parts differed by more than three elements they were considered as two different song types. If a song was already in the catalogue, we labelled it correspondingly; otherwise it was defined as a new type and included in the catalogue. To prevent erroneous entries, we checked the catalogue after completion for song types included twice. In addition, we also ensured that all songs labelled as belonging to a certain song type were indeed of that song type, by assessing them visually.

Data Analysis

To test whether the number of songs shared by a given number of males deviated from chance expectation, we used two different simulation approaches. The basic set-up of these simulations was that we constructed populations of tutors from which simulated scholars acquired their repertoires. In the first approach ('small population'), the 12 males of the study population were used as the generation of tutors. This approach has the advantage that the total repertoire of the study population is clearly defined, and that the

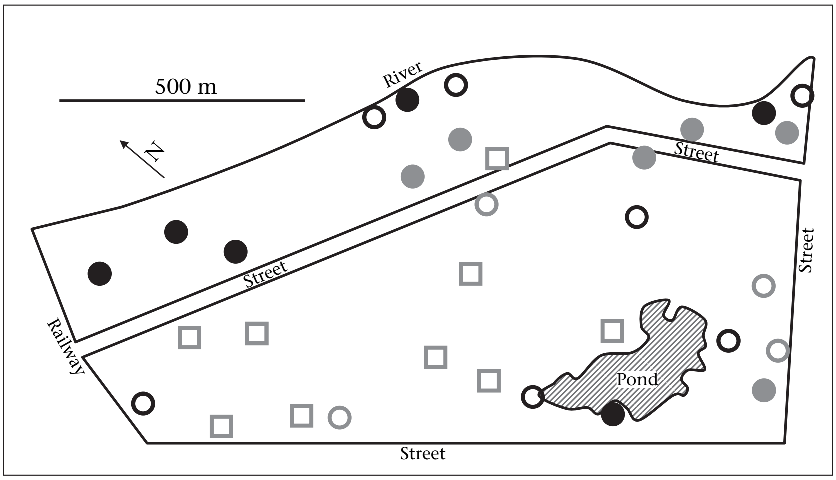

Figure 1. Sketch of the study site and locations of all territories in the year of the study (2004). Filled circles denote centres of territories of males included in the study; open symbols show centres of territories of males not included in the study (owing to lack of recording of sufficient duration, or males being in their second calendar year). Black symbols show males settling in the study area for at least the second year. Grey symbols show males in their second calendar year (squares) or males not obviously in their second calendar year (circles). The study site is split by a street and surrounded by a river (north), a railway or streets on the other three borders. Nearby habitat largely consists of urban living quarters, and private gardens. Closest nightingale territories outside the study site are ca. 1 km away and not within earshot of the males investigated.

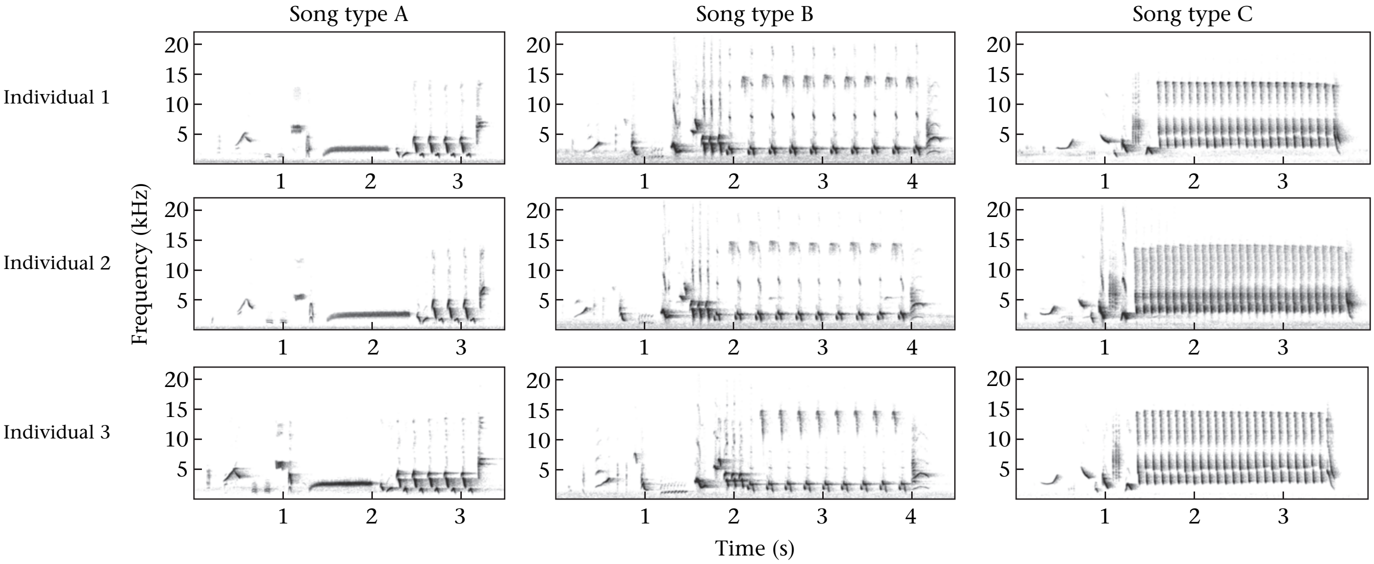

Figure 2. Sonagrams of three different song types sung by three different individuals. Songs were defined as belonging to the same type when their repetitive sections were identical with regard to composition and succession (disregarding the number of repetitions per element or syllable) and their initial nonrepetitive parts did not differ by more than three elements.

frequency of occurrence of song types within and across males can be adjusted to somewhat realistic values. This approach is based on the assumption that our study males encountered a situation during their song acquisition period that was similar to the one existent during the study year. That is, the properties of the repertoires our study males encountered were similar with regard to the total number of song types available, the number of males sharing different song types and the frequency with which males sang these song types. These assumptions seem reasonable for two reasons. First, nightingale song seems to be remarkably stable over longer periods of time and also over larger areas (D. Todt, H. Hultsch & R. Mundry, personal observations). Second, male nightingales seem to have a rather high probability of establishing breeding territories close to their natal territory (R. Mundry, C. Sommer & P. Sprau, unpublished data). It thus appears likely that the nightingales we investigated grew up in a situation similar to the one we found in the study year. However, this approach may underestimate the number of males from which a young male acquires its repertoire as well as the total number of song types sung by these males. It seems also likely that the total number of males from which a group of young birds acquires their repertoires is larger.

Hence we implemented a second simulation approach ('large population'). In this simulation we set the total number of tutors to 30 males (the approximate number of territories occupied per year in the study site), which were singing an estimated total repertoire size expected for this number of males (see below for details). This simulation has the advantage of being potentially more realistic with regard to the total number of tutors and song types available. However, the disadvantage of this approach is that the frequency of occurrence of song types in the population, as well as the total repertoire size of the population, does not necessarily match the natural conditions. To obtain realistic values for the total repertoire size in the population, we first determined total repertoire size of an infinite population from the saturation curve using the equation $R_i = C + a \times b^i$ (Bortz et al. 1990), where R_i is the total repertoire size after the ith analysed male, and C, a and b are the parameters of the saturation curve (with C being the asymptote). We then determined the expected repertoire size for 30 males using the above equation. To avoid this estimate depending on the sequence by which males are entered into the analysis, we randomized the sequence of males 1000 times and each time estimated the total repertoire size for 30 males. As about 10% of these estimates were smaller than or equal to the total repertoire size found in the 12 studied males, we discarded these values that were obviously too small, leaving 904 estimates of the total repertoire size, ranging from 464 (the total number of different song types we found in the studied males plus 1) to 748 (average: 514). From these, we randomly sampled (with replacement) the total repertoire size of the simulated population of 30 tutors. Songs of the total repertoire were then randomly assigned to the repertoires of tutors, with the random sampling restricted such that the desired total repertoire size was achieved. Repertoire sizes of the simulated tutors were randomly chosen (with replacement) from the repertoire sizes found in the studied males.

As scholars we generally simulated 12 males, each randomly incorporating song types out of the pool of available song types into its repertoire until a certain repertoire size was reached. The repertoire sizes of the 12 simulated scholars equalled those we found for the 12 studied males (mean = 187.8; range 146–222). For both approaches (small and large population) we implemented different choice models that differed in the probabilities with which different song types were chosen from the pool of available song types. In the first choice model ('type choice'), each song type had exactly the same probability of being included in a repertoire; in the second choice model ('repertoire proportional choice'), the probability of each song type being included in a certain repertoire corresponded to the number of tutors having this song type in their repertoire; in the last choice model ('performance proportional choice'), the probability of each song type being included in a certain repertoire corresponded to its summed frequency of occurrence in the songs of all tutors. We did not implement this latter choice model in the simulation approach with the large tutor population, as we did not have realistic assumptions about the frequency of occurrence of song types within and across tutors. In the simulations with a small tutor population, all three choice models existed in two versions: in one version ('unrestricted') each scholar independently chose song types from the pool available; in the other version ('restricted'), the choice from the pool was restricted such that the total repertoire of the scholars equalled that actually observed in the study population (463). The restriction was achieved by initially allocating each of the song types available to a randomly chosen scholar. We implemented the restricted version to ensure that we had simulated populations of scholars that did not differ fundamentally from the one actually observed in their total repertoire size. We did not implement the restricted choice in the simulation with the larger population of tutors, as this would have partly removed the effect of a larger number of song types available. In all simulations the simulated scholars' choice was further restricted such that each male could choose each song type at most once. Each simulation was repeated 1000 times and confidence intervals (2.5 and 97.5%) of the numbers of song types occurring in exactly one male, two males, etc. were derived using the percentile method (Manly 1997). All these simulations were programmed in R version 2.9.1 (R Development Core Team 2009) by R.M. The parameters of the saturation curve were determined with the aid of the R-function 'optim' and based on minimizing least squares.

We tested for saturation of the total repertoire by considering the number of 'new' song types each male added to the already existing catalogue. As this measure might be sensitive to the sequence in which males are added to the catalogue, we randomized the sequence in which subjects were added 1000 times (using a self-written R-script), by this means obtaining bootstrapped confidence intervals (using the percentile method; Manly 1997) of the number of songs added by a subject in a certain position in the list of the analysed subjects.

Simulated Cultural Evolution of Repertoire Sharing

In this investigation we simulated the cultural evolution of repertoire sharing in subsequent generations of males, each acquiring songs from the previous generation and inventing new song types with a certain probability. This time we used only one simulation approach corresponding to the large population approach. The initial populations were generated using the same methods as described above. We set survival probability (per time step, i.e. year) of males to 0.5 (the approximate return rate in our study population) and further restricted survival such that a male could remain in the population for at most eight time steps (the maximum observed in our study population). At each time step of the simulation, randomly chosen nonsurviving males and males exceeding the maximum age were removed and then replaced by newly entering males, which acquired their repertoires solely from the survivors of the prior time step. The probability by which a newly entering male incorporated a song type into its repertoire was either simple 'type choice', i.e. each song type having the same probability of being acquired, or 'repertoire proportional choice', i.e. the probability of each song type being included in a certain male's repertoire corresponded to the number of males that had survived from the previous time step and that had this song type in their repertoire. Note that the latter approach is conservative with regard to preferential choice of shared song types, as the preference for shared song types is a simple function of the proportion of males singing a song. Repertoire sizes of newly entering males were randomly chosen from the repertoire sizes observed in our study population. Additionally, we assumed that inventions of new songs could occur. Based on the results of the previous simulation, we systematically varied the probability of an invention happening from 0.01 to 0.1 (increment 0.01). These were probabilities per learning event, that is, each song acquired had this chance of being an invention. At each time step we evaluated the total repertoire size as well as the numbers of song types shared by different numbers of males (1–12) of 12 randomly chosen males. We simulated 1000 subsequent generations and repeated the simulation 500 times. Results were summarized using averages and confidence intervals (see above) across simulations. All simulations were run using programs written in R (R Development Core Team 2009) by R.M. The code was strongly based on a Java program provided by R. F. Lachlan (Department of Biology, Duke University).

RESULTS

Overall, the frequency distribution of the numbers of song types being shared by different numbers of males clearly differed from all simulated random choice models (Fig. 3). In fact, songs sung by a single male as well as songs shared by all the males or all but one male were generally more common than expected by chance. Furthermore, songs sung by an intermediate number of males were either less common than expected by chance or did not strongly differ from expectation. Different models of random choice had a marked influence on the expected number of songs being shared by a certain number of males, as had different approaches to simulate the generation of tutors. However, these differences had no impact on the general conclusion that songs shared by very many males as well as unshared songs were more common and

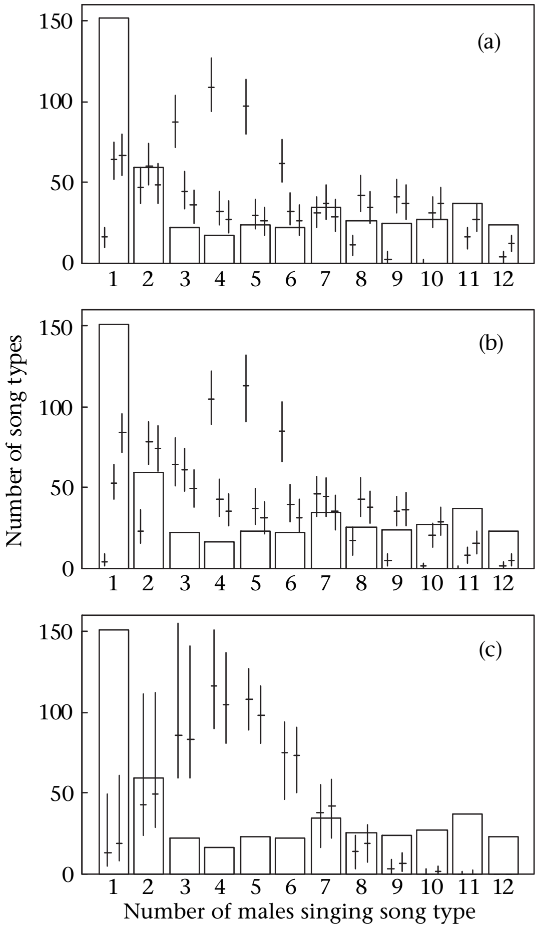

Figure 3. Number of song types (bars, *Y* axis) sung by a certain number of males (*X* axis) and corresponding expected numbers (crosses) assuming that males randomly choose their song types from a pool of available song types. Crosses depict median and percentiles (0.025 and 0.975) of different models of random choice. In (a) and (b) scholars chose song types from 12 tutors having the same repertoires as the studied males. Scholars chose song types with equal probabilities (left cross per bar), with probabilities corresponding to the number of tutors that sang the song types (middle cross per bar) and with probabilities corresponding to the summed frequencies with which all tutors sang the song types (right cross per bar). In (a) the choice was unrestricted; in (b) the choice was restricted such that each of the available song types occurred in the repertoire of at least one scholar. In (c) scholars acquired song types from a population of 30 males having an average total repertoire of 514 song types (range 464–748). Song types were randomly allocated to tutors, and tutors had repertoire sizes randomly sampled from those observed in the study population. Crosses depict simulations in which scholars chose randomly from the available song types (left cross per bar) or chose song types with a probability proportionate to the number of tutors sharing the type (right cross per bar). Bars are the same in (a), (b) and (c).

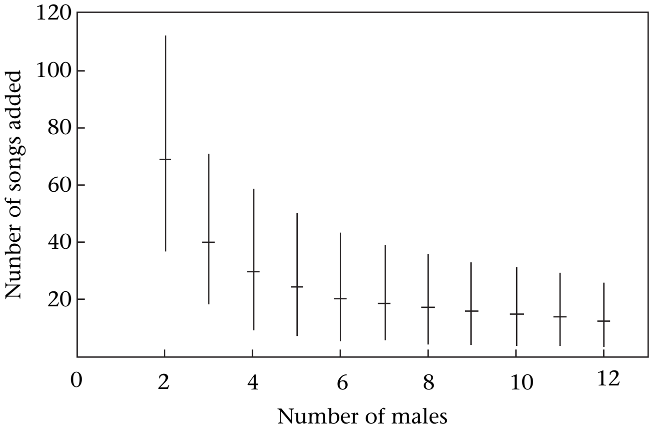

Figure 4. Number of song types males contributed to the total repertoire, as a function of their position in the sequence in which males were entered into the data set. Indicated are mean and confidence intervals (2.5 and 97.5%) derived from 1000 random sequences.

songs shared by intermediate numbers of males were less common than expected by chance.

From these results it can also be estimated at what rate innovations of songs would have to occur to achieve the number of unshared song types observed in our study males. Assuming that the total number of acquisition events is equal to the sum of all repertoire sizes observed, and taking the difference between the simulated and observed numbers of unshared song types as the number of inventions, it appears that innovations would need to occur at a probability of 0.052 per learning event (range across different simulation models: 0.029–0.065) to generate a number of unshared songs as observed. In absolute numbers of songs, this reflects ca. 10 innovated songs per male.

The total repertoire did not obviously saturate (Fig. 4). Instead, even the last male analysed added 12 song types to the total repertoire (average of 1000 randomizations), which corresponds to the average number of unshared songs per male (range 4–26 song types or 2.5–13%). In particular, the lower confidence interval of the number of added song types seemed approximately to level out after inclusion of nine males at a value slightly above eight, suggesting that each male added some unique song types to the repertoire of the population.

In most simulations of cultural evolution, the total repertoire size of 12 randomly chosen males, as well as the numbers of song types shared by a certain number of males, initially changed considerably but clearly stabilized after ca. 30–50 time steps. The following results are thus averages over the last 900 time steps. The total repertoire size of the 12 males clearly increased with increasing innovation rate, and was considerably larger in simulations with type choice compared with simulations with repertoire proportionate choice (Fig. 5). With one exception (repertoire proportionate choice and innovation rate = 0.01), the total repertoire of 12 randomly chosen males was clearly in excess of that found in our 12 study males. The number of unshared song types varied greatly with the simulated innovation rate and was largest when the innovation was at its maximum (0.1; Fig. 6). In the case of type choice even small innovation rates (ca. 0.02–0.03) led to numbers of unshared songs being larger than in the studied males, whereas in the case of repertoire proportionate choice this happened only at intermediate innovation rates (ca. 0.04–0.05). Song types shared by a smaller number of males (two to five) were almost invariably more common than found in the study population, and songs shared by a larger number of males (9–12) were almost always less common than in the study population. This was the case regardless of which choice model was used (type choice or repertoire proportionate choice) and which innovation rate was assumed.

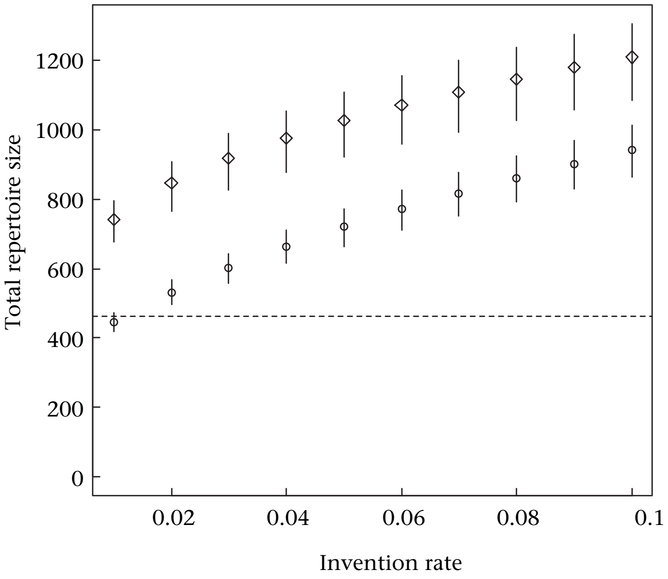

Figure 5. Total repertoire size of 12 randomly chosen males after simulated cultural evolution with different invention rates (i.e. probability of inventing a new song per learning event). In the simulation, newly entering scholars randomly chose song types from the pool of song types sung by the males present in the population. Circles denote results for simulations in which males chose songs with a probability proportionate to the number of males in the tutor population singing them, and diamonds show results obtained when males chose all songs with the same probability. Shown are medians (symbols) and confidence intervals (2.5 and 97.5%; lines) of 500 simulations, each being averaged over the generations 101–1000. The dashed line indicates the total repertoire size found in our 12 study males.

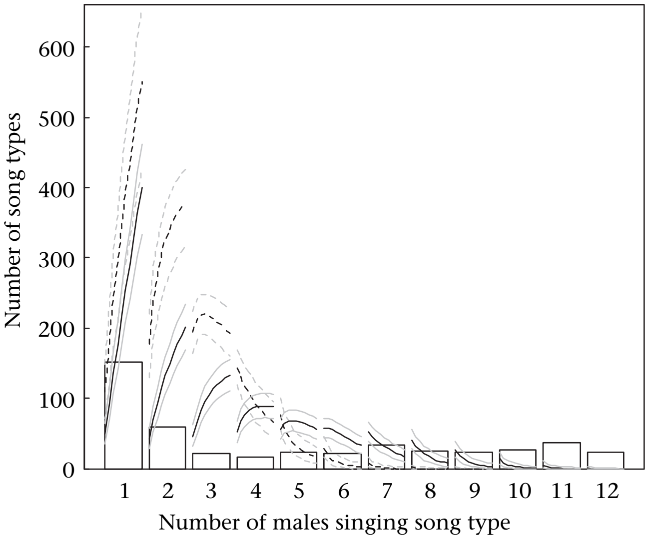

Figure 6. Number of song types (*Y* axis) sung by a certain number of males (*X* axis) after simulated cultural evolution with different invention rates (i.e. probability of inventing a new song per learning event; lines) and in the studied males (bars). The invention rate varied from 0.01 to 0.1 (increment 0.01) along each of the lines. In the simulation, newly entering scholars randomly chose song types from the pool of song types sung by the males present in the population. Lines show results for 12 males randomly chosen out of a population of 30 and an average initial repertoire size of 514 (range 464–748). Scholars either acquired all song types with the same probability (dashed lines), or with a probability proportionate to the number of tutors sharing them (solid lines). Repertoire sizes of the simulated males were randomly chosen from those found in the study population. Black lines indicate medians and grey lines confidence intervals (2.5 and 97.5%) of 500 simulations, each being averaged over generations 101–1000.

DISCUSSION

Our first simulation revealed that the observed distribution of songs across males differed strikingly from expectation. Regardless of what specific random choice model or population size we applied, we found clearly more song types than expected that were shared by many males and also more song types than expected that were sung by a single male only.

The finding that more songs than expected were shared by most males suggests that nightingales have a preference to incorporate those songs into their repertoires that are shared among many males in their local neighbourhood. This conclusion was supported by the cultural evolution simulations, which showed that, even when scholars acquired song types with a probability proportionate to the number of males sharing a song, songs sung by 12 males would be very rare. Hence, nightingales seem to be similar to song sparrows, for which it has been shown that young males preferentially incorporate those song types that are shared in the local population into their repertoire (Beecher et al. 1994; Nordby et al. 2000). As nightingales are known to song type match during vocal interactions (Todt 1971), acquiring shared songs probably functions in enabling song type matching (whether nightingales also use repertoire matching in vocal interactions is not yet known).

More surprising is the occurrence of so many song types being unshared, that is, sung by a single male only. This finding suggests that the preference for the acquisition of songs shared by many males is somewhat limited, such that not only songs shared by many males are acquired. Several, not mutually exclusive, mechanisms seem plausible by which such a limitation could be achieved, with the most simple one being not really a 'mechanism' in itself, but simply a limited capacity for the accurate copying of model song types. However, laboratory studies demonstrated that male nightingales can acquire at least 60 song types in their first sensitive phase of song learning (Todt & Hultsch 1998), and studies of wild birds revealed they had repertoires of between ca. 70 and 190 song types in their first breeding season (Kiefer et al. 2006, 2009). It is hence tempting to speculate that unshared songs are acquired through an active process and do not just arise through copying errors. A second potential mechanism by which such a limitation could be achieved is a preference for also acquiring songs that are shared by very few males only (similar to 'anti-conformity' as defined by Mesoudi & Lycett 2009). However, this seems rather unlikely to us, given our finding that the total repertoire size did not clearly saturate. In fact, assuming that nightingales incorporate into their repertoire only songs actually sung by conspecifics, one would expect the total repertoire of a population to saturate with increasing number of subjects investigated. In our study subjects, however, this did not seem to happen. A third mechanism that might explain the huge numbers of unshared songs in the population is invention of novel songs, and modification or recombination of learned songs, respectively. In fact, laboratory studies have demonstrated that nightingales do invent novel song types, which they either build de novo (Hultsch et al. 1998) or by recombination of parts of song types that they heard during the auditory phase of song acquisition (Hultsch 1990). Such recombinations of songs were also suggested for chaffinches, *Fringilla coelebs* (Slater & Ince 1979; Lachlan & Slater 2003), and wild song sparrows modify certain shared song types during song development, such that they become more individually distinctive (Nordby et al. 2007). As in the repertoires we investigated we occasionally found song types seemingly being a modification or recombination of parts of other song types (qualitative observations), it seems plausible that this also happens in free-ranging nightingales, even though we cannot rule out de novo inventions. This suggests that recombinations or modifications might actually be an active mechanism for achieving some unshared or individually distinctive songs rather than being copying errors (Nordby et al. 2007). The interpretation of unshared song types being recombinations, modifications or inventions is supported by the fact that the frequent occurrence of song types being unshared or shared only among a few males shows a striking similarity with the power law-like distributions found in several cultural traits of humans, which, it is suggested, arise through a combination of random copying and cultural mutation (i.e. 'invention'; e.g. Hahn & Bentley 2003; Bentley et al. 2004; Mesoudi & Lycett 2009). Finally, it seems possible that unshared song types arise though immigration of males from other populations. This seems plausible, as in each breeding season some fully mature males, presumably in at least their second breeding season, newly enter our study site, suggesting that some exchange with other sites does exist. In addition, several studies have demonstrated immigration to be a likely mechanism for the occurrence of rare or unshared song types (e.g. Slater & Ince 1979; Slater et al. 1980; Sorjonen 1987; Lynch et al. 1989; Lachlan & Slater 2003). However, in our subjects the proportion of unshared songs did not obviously differ between newly entering males (median: 3.9%; range 3–13) and males settling in the park for at least the second season (median: 7.6; range 2.5–12.5; Mann–Whitney U test: $U = 12$, $N_{\mathrm{new}} = N_{\mathrm{old}} = 6$, $P = 0.39$). Hence, although immigration seems a likely source of rare or unshared song types, it remains unclear to what degree this mechanism actually accounts for their occurrence. In addition, nightingale song seems to be remarkably stable over larger areas (D. Todt, H. Hultsch & R. Mundry, personal observations), male nightingales seem to have a rather high probability of establishing breeding territories close to their natal territory (R. Mundry, C. Sommer & P. Sprau, unpublished data) and adult male nightingales in our study population show high breeding site fidelity (S. Kiefer, S. Kipper, R. Mundry, C. Sommer, P. Sprau & M. Weiss, unpublished data). Overall, it thus seems likely to us that the invention of novel song types or modification of existing ones accounts at least to some extent for the large number of unshared song types.

The results of the cultural evolution simulation partly support our conclusions. With regard to the frequency of occurrence of song types shared by many males, all simulations revealed much smaller numbers than observed in our study population, suggesting that nightingales indeed have a clear preference to acquire songs types shared by many males. With regard to the number of unshared song types, the results were not as clear, as the results of our simulations varied greatly depending on which choice model and innovation rate were assumed. It is remarkable, however, that the simulation with repertoire proportionate choice and an innovation rate similar to the one estimated from our first simulation (0.05) revealed numbers of unshared songs that were very similar to the one we found in the study population. However, even this setting did not reveal numbers of song types shared by a smaller number of males (i.e. two to five) that were comparable with those found for the studied males. There is some considerable uncertainty with regard to the degree to which the simulations reflect aspects of the actual situation, such as the total repertoire size of the tutor population, or the potential influence of immigrants. In fact, a similar pattern with regard to the occurrence of unshared songs may arise through immigration of males 'bringing' new songs into the population. A particularly important discrepancy might be the number of tutors from which songs are acquired. In our simulations males simply acquired each song independently from all others from the total pool of the available song types. It seems plausible, however, that individual males in reality learn several song types from a single tutor and also that different males acquire songs from the same tutors. Such an acquisition process might lead to reduced numbers of song types shared by a few males. Nevertheless, it is remarkable that the initial simulation, as well as that of cultural evolution, suggested mutations or innovation to happen at a rate of ca. 0.05. Lachlan & Slater (2003) also estimated the upper bound mutation rate for chaffinches to be 0.05 (but see Slater et al. 1980). In any case, all simulations suggest that some invention of novel songs is involved, particularly as in repetitions of the cultural evolution simulations with a mutation rate of zero unshared songs rapidly disappeared more or less completely (results not shown). Finally, in almost all simulations of cultural evolution the total repertoire size increased considerably, suggesting that the actual situation and acquisition mechanisms are different from those simulated. Potentially, more realistic simulations based on a larger empirically studied population and allowing for exchange between neighbouring populations, as conducted by Lachlan & Slater (2003), could overcome this discrepancy.

The fact that results of both our analyses suggest that unshared songs are unlikely to appear through random copying from a pool of available song types but appear through invention of novel song types, modification of existing ones and/or immigration of males (in which case unshared song types might be retained by the males to some extent) makes it tempting to speculate about whether these unshared song types have a functional significance. The possible (not mutually exclusive) functions of unshared song types could be that they: (1) enable individual recognition; (2) allow for de-escalating vocal interactions; and (3) make it impossible to be matched. However, enabling individual recognition (as suggested for song sparrows; Nordby et al. 2007) seems unlikely to be the primary function of unshared song types in nightingales. Given their large individual repertoires, a recognition based on unshared (i.e. individual-specific) song types would require the ability to process large amounts of information, making recognition based on voice cues (Weary & Krebs 1992), for example, more plausible. In addition, the proportion of unshared songs in the individual repertoires was actually rather small (average: 6.5%, range 2.5–13%) and hence limited their temporal availability for individual recognition. An alternative function of unshared song types could be that they allow for de-escalating vocal interactions, as shown for song sparrows (Beecher & Campbell 2005). Whether nightingales sing unshared song types as a de-escalating signal cannot be answered at this stage and thus remains to be tested in future playback experiments. Finally, it seems possible that nightingales sing unshared songs to avoid being matched. One possible function of avoiding being matched could be that the frequency by which males match and are matched might correlate with their repertoire size and hence allow for a quick assessment of a male's repertoire size, as suggested by Kiefer et al. (2006). As repertoire size in nightingales is correlated with putative measures of male quality (Kipper et al. 2006), the frequency by which two males match one another might allow for a rapid assessment (by eavesdropping females and males) of the relative quality of two interactants. Consequently, males engaged in vocal interactions during the pairing season should exhibit a preference to sing both shared songs (when matching the opponent) and unshared (i.e. individual-specific) songs to avoid being matched by the other.

Taken together, our findings strongly suggest that the distribution of songs across males we actually found is not the result of an acquisition process that just incorporates song types at random or is proportionate to the number of males who share them. Instead, it seems that nightingales have some bias towards conformity and anticonformity at the same time, that is, a tendency for a preference to acquire common as well as unshared songs. Unshared songs may arise through immigration of males from other areas or through invention, but to what extent such inventions are actually de novo inventions or modifications and/or recombinations of already existing song types remains unclear. The function of this twofold preference might be to attain partly shared repertoires, enabling matching, while at the same time preventing large similarities between repertoires, enabling avoidance of being matched.

Acknowledgments

We thank the Berliner Senatsverwaltung für Stadtentwicklung und Umweltschutz for the permission to capture birds and the Vogelwarte Radolfzell (Beringungszentrale an der Max-Planck-Forschungsstelle für Ornithologie) for their cooperation. We are greatly indebted to Sarah Kiefer, Silke Kipper, Christina Sommer, Christoph Teufel and Sylvia van der Woude for their assistance in bird netting and/or obtaining recordings. Henrike Hultsch and Christina Sommer provided very helpful comments on the manuscript, and Philipp Sprau thanks Silke Kipper for valuable input during an earlier stage of this project. We also thank Constance Scharff for support in various ways and Dietmar Todt as well as Henrike Hultsch for many very inspiring discussions about nightingale song. Finally we thank Diego Gil, Robert F. Lachlan and Michael D. Beecher for very helpful and constructive comments on the manuscript and Robert F. Lachlan for kindly providing the Java program.

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