


Songbird presumed to be age-limited learner may change repertoire size and composition throughout their life

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Abstract

Songbirds learn to sing by imitating their conspecific songs through social learning. It is commonly thought that in species with small repertoires, so-called crystallization of the song repertoire takes place before the first breeding attempt and afterwards their repertoires remain unchanged. However, the number of studies in which individual song repertoires have been tracked longitudinally under natural conditions is still small. The ortolan bunting (*Emberiza hortulana*) is a small Eurasian passerine species. Studies on this species have shown that males have small song repertoires (usually 2–3), share the same final phrase within a local dialect area, and their repertoires remain unchanged during their lifetimes. We studied the whole, isolated Norwegian population of this species with 100–150 individually marked males. We compared repertoire sizes and contents using cross-sectional and longitudinal approaches. We focused on marked males aged 2–10 years and recorded in up to five breeding seasons between 2001 and 2006. There was no local dialect because songs with different final phrases occurred both within and between males. Repertoire size varied between 1 and 24 (4.7 ± 3.4) song types per male. Longitudinal analysis showed an increase in repertoire size in 29% and a decrease in 21% of males. Males whose repertoires remained the same in size between years often substantially changed in contents. New song types appeared in almost 70% of males, and over 30% of males started singing new syllable types after the second calendar year. In almost 50% of males, new song types appeared that were built as new combinations of syllables shown in previous years. In 30% of males, the song complexity increased with age. Simultaneously, over 60% of males selectively ceased singing some song types. We suggest that these repertoire alterations are linked to the isolation and fragmentation of this population, which may affect song learning patterns through increased breeding dispersal and a strongly male-biased sex ratio. Similar studies from abundant and continuous populations of the species are needed to test this idea.

Introduction

The song of songbirds (*Oscines*) is a sexually selected and culturally transmitted trait, which plays a crucial role in territory defence and mate attraction (Catchpole & Slater, 2008). Bird song is one of the best models for studying cultural evolution and has relevance beyond birds, by helping to understand vocalizations in other groups of animals such as cetaceans, bats, elephants and humans (Beecher & Brenowitz, 2005; Goller & Shizuka, 2018). A common feature of culturally transmitted traits is not only the necessity of transmission through imitation but also an interplay between inherited limitations (e.g. structure of vocal apparatus) and ecological processes affecting learning (e.g. population structure or dispersal

pattern). Regional dialects, long-term signal stability or even the sudden appearance of new memes are phenomena observed in bird song. These seem equivalent to other behaviours including tools use in chimpanzees or New Caledonian crows, the opening of milk bottles in parids or cultural revolutions in humpback whales *Megaptera novaeangliae* (Whiten *et al.*, 1999; Allen *et al.*, 2018; Aplin, 2019). Studies on culturally transmitted traits in most cases show the qualitative and/or quantitative status of these traits (e.g. prevalence in a population or populations), while much less is known about the changes over the course of an individual's life. Song is also a uniquely complex trait as it may vary in several dimensions simultaneously (e.g. acoustic structure, duration, amplitude, pattern of production in time and space). One of the

most conspicuous parameters of the song output is repertoire size. Repertoire size can be measured as the number of different syllables or song types a bird can produce depending on the duration, complexity and repeatability of song phrases produced in a species. Repertoire size seems to evolve under different selection pressures. In some species, females prefer mating with males having larger repertoires, which suggests that larger repertoires may indicate males of higher quality (e.g. in sedge warbler *Acrocephalus schoenobaenus*, Buchanan & Catchpole, 1997; great reed warbler *Acrocephalus arundinaceus*, Hasselquist, Bensch & von Schantz, 1996). In others, the level of repertoire sharing with neighbours seems to be more important than repertoire size. For example, in the song sparrow, *Melospiza melodia* sharing more songs with neighbours was advantageous in male–male interactions and territory tenure in some populations (e.g. Beecher, Campbell & Nordby, 2000). However, in this species, both the frequency of song sharing and whether it is advantageous in territorial defence differs among populations (Hughes *et al.*, 1998, 2007). It is also possible that both repertoire size and level of song sharing are simultaneously selected, for example if females prefer both better quality males (i.e. with larger repertoire size: Hasselquist *et al.*, 1996), and local males (i.e. with larger level of sharing: Węgrzyn & Leniowski, 2010, or performing shared syllables more precisely: Węgrzyn, Leniowski & Osiejuk, 2010).

Regardless of the character of the selection pressure on song repertoire size and sharing, both traits are also an outcome of learning patterns characteristic for a species or a population (e.g. migratory and sedentary populations may differ with respect to song acquisition and consequently in repertoire size and song sharing too, Ewert & Kroodsma, 1994; Handley & Nelson, 2005). Songbirds are usually divided into ‘open-ended learners’ and ‘age-limited learners’ (Beecher & Brenowitz, 2005). Birds belonging to the first group are able to increase repertoire size with age and these are usually species with repertoires of dozens or even hundreds of syllables (e.g. starling *Sturnus vulgaris* Eens, Pinxten & Verheyen, 1992a, 1992b). The ‘age-limited learners’ acquire repertoires during a limited time period when they are juveniles and after crystallization, their repertoires remain fixed for the remainder of their lives (Williams, 2004). However, such a rigid division of learning patterns may in reality hide a much more complex and diversified behaviour (Kipper & Kiefer, 2010; Mamede & Mota, 2012). The majority of songbirds have small or moderate repertoires, and so are usually implicitly regarded as ‘age-limited learners’ (Beecher & Brenowitz, 2005). However, detailed studies on song learning development that support this are only from a few model species. The number of studies indicating that the so-called ‘age-limited learners’ may have a much more flexible learning program and that their repertoires may change after first year of life is growing (McGregor & Krebs, 1989; but compare also Rivera-Gutierrez, Pinxten & Eens, 2011). Surely, there is a paucity of longitudinal data on song repertoire changes from wild populations of birds (Kipper & Kiefer, 2010; Mamede & Mota, 2012).

In this long-term study, we focused on the changes in repertoire size and composition in the ortolan bunting (*Emberiza*

hortulana). Early studies of this species focused mostly on song dialect characteristics (see Cramp & Perrins, 1994). Based on these earlier studies, the ortolan bunting was considered a typical ‘age-limited learner’ with a small repertoire of 2–3 song types, fixed for the lifetime period. This has been confirmed by one longitudinal study (Conrads, 1986). However, the latter study had a critically small sample size. Here, we studied a very specific population of the ortolan bunting at the edge of the species’ range in Norway. This population is heavily fragmented, isolated and has been under continuous decline for the last 60 years. Initially, the decline was probably an effect of human-induced changes in agriculture; however, in the last decades, the main reason for the decline should be linked to a biased sex ratio in this population (Dale, 2001). Due to female-biased natal dispersal, males from this population typically return to the population after wintering in Africa, whereas a large proportion of the females do not return to the population, resulting in an average 50% of unpaired males (Steifetten & Dale, 2006). Thus, despite high survival of males and high breeding success, only a fraction of the males reproduce, which is not sufficient to keep population size stable (Dale, 2001; Steifetten & Dale, 2006). The lack of females and patchiness of the population has an additional effect on the behaviour of the males. Males who fail in attracting a female often change the location of their singing within a breeding season and between seasons (Dale, Lunde & Steifetten, 2005; Dale *et al.*, 2006). Thus, they sequentially change their social environment and defend territories among different sets of neighbours with potentially different song repertoires. Here, we study age-related changes in song repertoire size and composition in this presumably ‘age-limited learner’ with a small repertoire and relate the findings to the specific ecological conditions of this population.

Material and methods

Study population

From 2001 to 2006, we studied colour-marked ortolan buntings in Hedmark county, south-eastern Norway (60.29–60.53°N, 11.40–12.18°E). The study area covered the main part of the ortolan bunting distribution range in Norway. Ortolan buntings occurred in 30 sites within an area of about 500 km². The total number of males in the population declined from about 151–155 in 2001 to about 104–110 in 2006, and the majority of them were colour-ringed (see Steifetten & Dale, 2006 for details). We recorded birds in all known inhabited patches, and all suitable habitats (raised peat bogs, forest clear-cuts, land being cleared for cultivation, burnt forest etc.) were regularly inspected during the breeding season in order to find buntings in all potential habitat patches. It was not always possible to record the song of all birds at a particular site, but the number of birds recorded was proportional to the total number of territorial males at a particular site. Regardless of the recording, each male was localized and individually recognized within our study area at least every third day during the breeding period. During these observations, the pairing status of each male was noted.

Song recordings

Birds were recorded between 04:00 and 11:00 local time, by using HHB PDR 1000 Professional DAT, Sony TCD-D8 DAT, Aiwa HS-200 DAT and Marantz PMD 670 solid-state recorders coupled with Telinga V Pro Science parabola or Sennheiser ME 67 shotgun microphones. Recorded birds were individually recognized by colour rings, if possible, using a telescope (description of procedures in Osiejuk *et al.*, 2003a). Positions of all recorded males were marked on sketch maps, and the geographic coordinates were recorded using GPS receivers.

Song analysis

All recordings were done using 48 kHz/16 bit sampling and were analysed with Avisoft SASLab Pro 4.1 (and later versions) software with the following set of parameters: 1024 FFT-length, Frame (%) = 25, Window = Hamming and Temporal Overlap = 87.5%. This gave a 244 Hz bandwidth with 42 Hz frequency and 2.9 ms time resolution (Specht, 2010). The songs were described using single syllables as minimal units of song production defined as the smallest invariant units in a male's repertoire (Podos *et al.*, 1992). Consequently, each recorded song was divided into syllables and we described different song types using letter notation, for example *aaaabb* or *eeeehff*, where letters denote particular syllables. In this paper, we use the term 'song type' to indicate a group of songs that consist of the same syllables arranged in the same order, for example *ab* and *ehf* notations reflect two song types presented in previous sentence. The idea of song type classification is presented graphically on Fig. 1, where squares with different fills represent different song types. It is later used to illustrate changes in repertoire composition. The detailed methods of sonogram analysis and rationale for song type description are provided elsewhere (Osiejuk *et al.*, 2003a). The song type

classification method we applied here distinguished a little more song types than previous methods (e.g. Conrads, 1986). The difference being that Conrads (1986) method worked in a population where all males shared the same final phrase, let's give it a *b*-phrase. Thus, he treated *a*-song as a shortened version of *ab*-song type. We treat both *a*- and *ab*-songs as two different song types as we know that some males may sing the initial *a*-phrase together with a final phrase different than *b*-phrase. We analysed syllable and song type repertoire changes by comparing their sizes and contents in consecutive breeding seasons.

Sample size

Altogether, we recorded and analysed over 37 thousand songs from 1264 recordings for 400 individuals. It was not possible to individually recognize every recorded male or acquire enough song samples to reliably estimate the repertoire size for every male. Therefore, we used subsamples of all of the material recorded in subsequent analyses.

In cross-sectional analyses devoted to estimating repertoire size variation, we used recordings of 143 different males of known age for which we had recorded over 100 songs. This was a very restrictive assumption as ca. 50 songs per male appears to cover the whole repertoire (own data including whole day recordings of marked birds with microphone array system (Skierczyński, 2009).

In the longitudinal analyses of repertoire size changes, we focused on colour-ringed males with known age and over 100 songs recorded per year. We separately analysed (1) males with an exact known age (i.e. ringed as nestlings: age 2K-10K, $N = 39$, where 2K means bird in second calendar year of life and so on), and (2) all recorded, ringed males, meaning that there were birds with an exact known age as well as bird of minimum known age, among them (i.e. ringed as adult

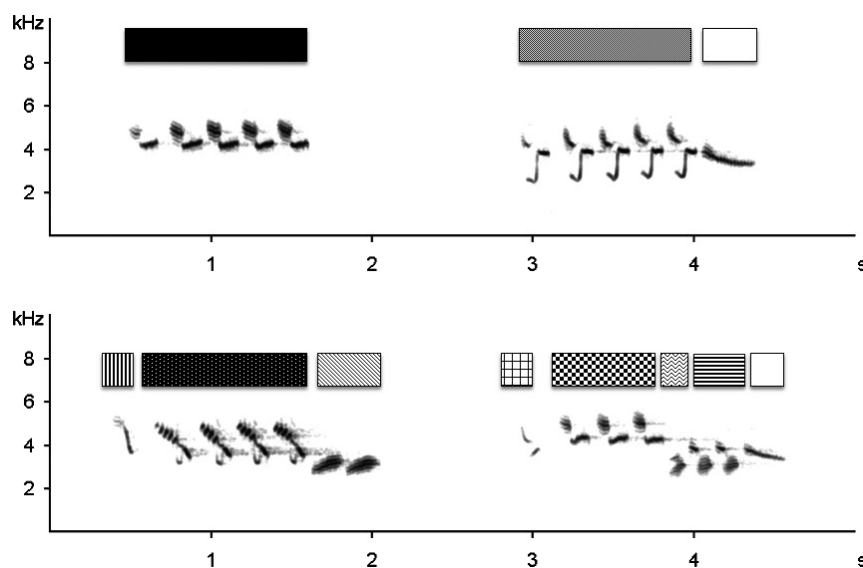


Figure 1 Sonograms of the ortolan bunting songs from the Norwegian population. Filled squares indicate different syllable types building songs.

2K+, $N = 135$, where 2K+ means that bird was at least in second calendar year or older).

Longitudinal comparison of repertoire composition was done for colour-ringed males of known minimal or exact age (age 2K–10K and $\geq 2K+$, $N = 51$) and recorded in 2–5 seasons during 2001–06. We only used recordings in which the identity of the recorded male was confirmed by observation of the colouring combination during the time the recording occurred (usually by the second observer with a telescope). Although this decreased the sample size used for analyses, this ensured that repertoires were assigned to the correct individuals.

Statistical analyses

Our analyses were focused on repertoire size and composition changes with age. As repertoire size had a positively skewed distribution, we built models with log-transformed repertoire size as the dependent variable. In cross-sectional analysis of repertoire size variation, we used data from each male from a single season selected randomly in order to avoid pseudo-replication. Cross-sectional analyses may, in general, hide the true nature of changes with time. For example, it may show that repertoire increases with age, whereas in reality repertoire size may not change with age but individuals with smaller repertoires do not live as long (Forstmeier *et al.*, 2006). Therefore, we used the smaller number of longitudinally tracked individuals to test age effects on repertoire size more explicitly. Longitudinal analyses were carried out by means of generalized mixed models (later GLMM) assuming normal error distribution of log-transformed repertoire size and a log-link function. Male identity was included as a random factor. Results are reported as z -scores with P value and estimate $\bar{x} \pm SE$. P -values are two-tailed, unless otherwise stated. Means are quoted as $\bar{x} \pm SE$ throughout. All statistics were calculated by STATA 15 software.

Results

Cross-sectional analysis revealed that repertoire size varied between 1 and 24 song types ($\bar{x} \pm SE = 4.8 \pm 0.29$, 95% CI = 4.2–5.3, $N = 143$) per male. The repertoire size distribution was positively skewed. Therefore, we used linear regression to test for the effect of age on log-transformed song type repertoire size, but no directional change was found ($\beta \pm SE = -0.04 \pm 0.034$, $t = -0.10$, $P = 0.919$; Fig. 2).

Longitudinal comparisons revealed that there was no directional change in repertoire size with age (GLMM for males with exactly know age: $\beta \pm SE = 0.01 \pm 0.025$, $z = 0.45$, $P = 0.654$, $N = 51$, 95% CI = -0.037 – 0.059 ; and for males with at least their minimum known age: $\beta \pm SE = 0.003 \pm 0.009$, $z = 0.31$, $P = 0.754$, $N = 135$). We found that repertoire sizes for some males remained stable while in others it decreased or increased and such changes were observed for males of different ages, not only in those that are just after their first calendar year of life (Fig. 3).

The comparison of a males' repertoire composition in subsequent years revealed that there were several mechanisms responsible for the observed changes. The increase in song type repertoire size was related to the fact that some males

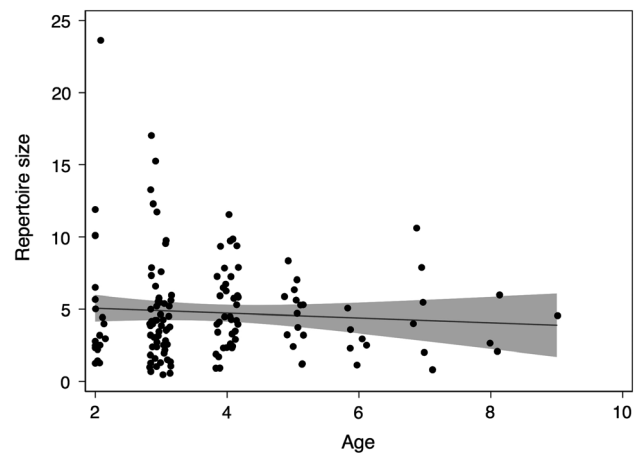


Figure 2 Relationship between males' age and repertoire size of ortolan buntings (linear prediction and 95% CI) illustrating cross-sectional analysis. Each dot represents a different male ($N = 143$). Jitter has been added to age markers to better illustrate numbers of males with particular repertoire size and age.

started singing new syllable type(s) and as a consequence new song type(s) after the 2K age (further called novelty; Fig. 4). Song type repertoire also increased because some males recombined syllables from the song types they already possessed and started singing a new combination of syllable sequences, that is new song types according to our nomenclature (further called recombination, Fig. 4). The recombination and novelty occurred independently or together and were often connected with an increase in song type complexity as some new song types were built using a larger number of different syllables

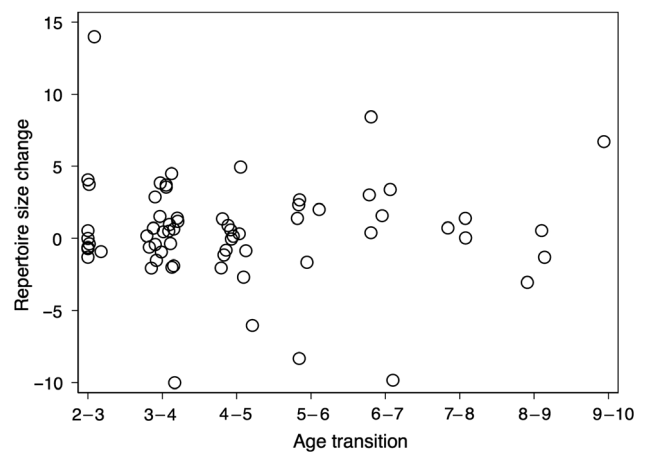


Figure 3 Illustration of repertoire size changes with age in ortolan buntings. Circles indicate how repertoire size changed (e.g. -3 on y -axis means that a male lost 3 song types in comparison to previous year, 0 means that repertoire size remained the same etc.). Age transitions on the x -axis indicate a point of time used for comparison, for example 2–3 means that circles indicate what happened to repertoire sizes of males in age 3K in comparison to their repertoire in age 2K and so on.

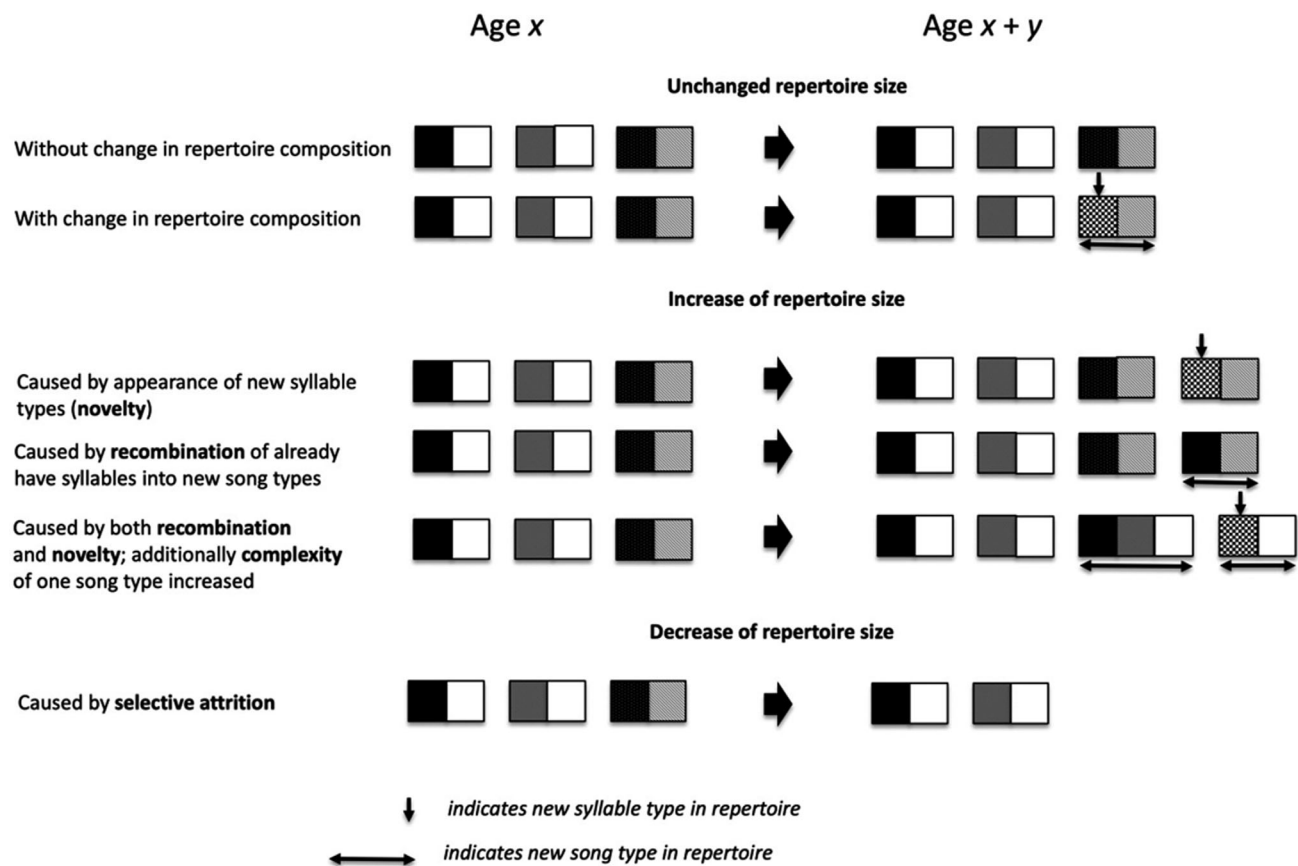


Figure 4 A schematic illustration of repertoire changes over time observed in the Norwegian population of ortolan buntings. Blocks of filled squares represent syllable types (see Fig. 1). Increase, decrease or unchanged repertoires are products of denoted mechanisms: novelty, recombination and selective attrition. As indicated an increase in song complexity might be a result of both novelty and recombination.

(Fig. 4). A decrease in repertoire size was observed as some males selectively ceased to sing certain song types (further called selective attrition; Fig. 4). These different processes were observed together or alone for different males and across different years. Therefore, there were several males whose repertoires remained the same in size between study years but their repertoire composition changed. New syllable types were found in the repertoires of 16 males and new song types in the repertoires of 35 males among a total of 51 males observed longitudinally (Fig. 4). For males with new syllables after 2K, we found from 1 to 5 new syllable types in their repertoires ($\bar{x} \pm \text{SE}$: 1.9 ± 0.31 , $N = 16$). Males with new song types after 2K produced from 1 to 16 different and new song types ($\bar{x} \pm \text{SE}$: 3.2 ± 0.54 , $N = 35$). Novelty and recombination ($r_s = 0.35$, $P = 0.011$, $N = 51$) as well as novelty and an increase in song complexity ($r_s = 0.27$, $P = 0.054$, $N = 51$) were weakly but significantly or almost significantly correlated. The strongest relationship was found for recombination and an increase in song complexity ($r_s = 0.52$, $P < 0.001$, $N = 51$). Altogether, in ca. 10% of the males, we observed a clear increase in repertoire size (on average from less than 4 to over 11 song types) and in ca. 20% of males, repertoire size decreased (from around 9 to less than 6 song types) with the remaining 70%

having a stable repertoire size of around 3–4 song types. However, in the last circumstance, it does not mean that there was no change in repertoire composition across the years. For only 31% of males, we did not observe changes in repertoires related to appearance of new syllables or song types. It is worth noting that the same song types were faithfully reproduced in subsequent years (Fig. 5).

One of the males exhibited a very specific pattern of song repertoire change. During his first breeding season, he only sang songs clearly resembling, and so learned, from a yellowhammer *Emberiza citrinella* tutor (such behaviour has also been observed earlier in this species: Osiejuk *et al.*, 2003b, 2004; Jakubowska, Łosak & Osiejuk, 2015). In the following season, he modified his repertoire, stopped singing some of the yellowhammer-like phrases and started singing typical phrases of the ortolan bunting (Fig. 6).

Discussion

We found compelling evidence that males of the ortolan bunting, a presumably 'age-limited learner' with a small repertoire size, are able to possess much larger repertoires than previously reported (Conrads, 1986; Cramp & Perrins, 1994) and

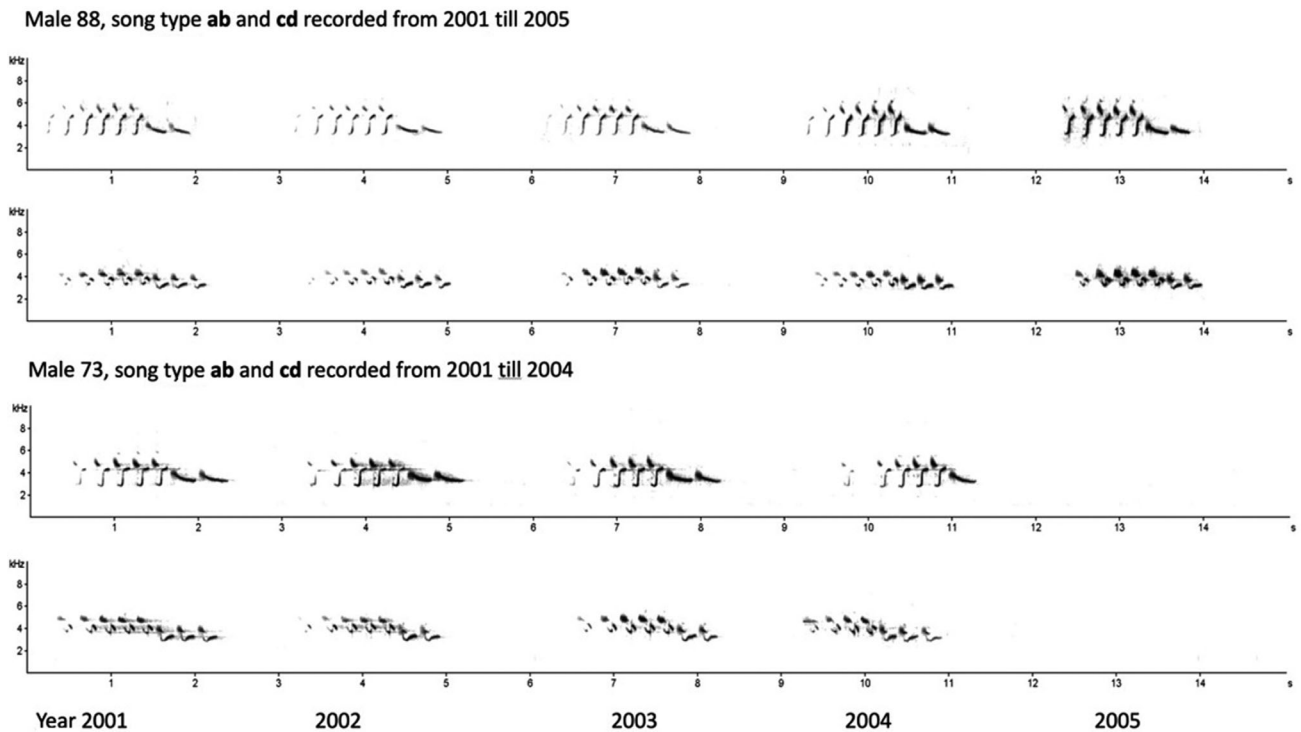


Figure 5 Sonograms of the common song types (ab and cd) derived from repertoires of two males (no. 73 and 88) who sang them in years 2001–2005.

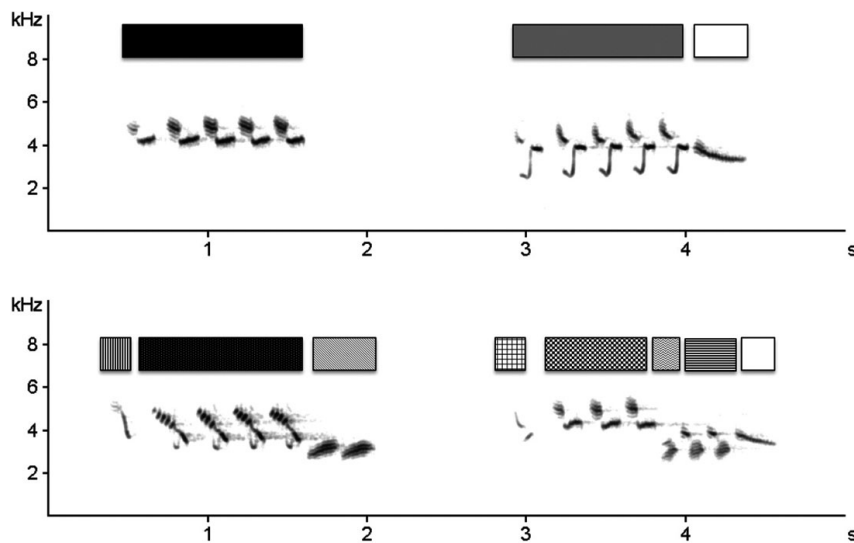


Figure 6 Sonograms of the ortolan bunting songs derived from repertoire of a male who initially sang only imitations of yellowhammer phrases (EC), and in the following season matched his own species song template (EH).

can modify their repertoire composition between seasons in several different ways, including the acquisition of new song types. Although we cannot make direct comparisons with other populations studied with the same methods, there are no

reports in the literature of any other population of ortolan buntings with anything close to the repertoire size we found (Cramp & Perrins, 1994). We suggest that changes in the environment (isolation, fragmentation), population ecology (male-

biased sex ratio) and behaviour (longer breeding than natal dispersal) may affect song learning and repertoire use patterns, thereby explaining why the Norwegian population differs from all those previously studied.

Most previous studies showing longitudinal changes in repertoire size or composition concern species with large repertoires (e.g. common nightingale *Luscinia megarhynchos* Kipper *et al.*, 2004; Kiefer *et al.*, 2009, 2010; canary *Serinus canaria* Leitner *et al.* 2001, great reed warbler Węgrzyn & Leniowski, 2010; serin *Serinus serinus* Mamede & Mota, 2012). Such species belong to 'open-ended learners' where it is expected that repertoires change between years. On the other hand, the character of the observed changes was often differentiated. In some cases, the increase in repertoire size with age was attributed to individual differences in genetic quality or nutritional stress during development (e.g. Hasselquist *et al.*, 1996; Buchanan *et al.*, 2003). In others, the composition of repertoires seems to reflect male–male interaction where sharing more common structures is more important than an increase in repertoire size (Kipper *et al.*, 2004; Kiefer *et al.*, 2010; Węgrzyn & Leniowski, 2010).

Songbirds with small or moderate repertoires have rarely been the subjects of longitudinal studies in the field designed to answer the questions, relating to if and how their repertoires change with age. This is surprising as more than 20 years ago, McGregor & Krebs (1989) showed that great tits *Parus major* extend the time of song learning beyond their first year in order to acoustically match their neighbours. Male ortolan buntings are also able to match neighbours acoustically by singing shared song types (Skierczyński, 2009). The most important question is if sharing occurred because they learned a larger set of songs after hatching and then only used a part of their repertoire (selective attrition, see next paragraph), or if they are really able to acquire new song types after the first year of life? The last hypothesis is supported by the observation of a male which, during his first breeding season, only used yellowhammer-like song types, but later started singing typical ortolan bunting songs. The fact that mimicking other species was found in the studied population is not new. It has been shown earlier that some males are able to acquire song structures from the related yellowhammer or even the unrelated redwing *Turdus iliacus*, which is common in this environment (Osiejuk *et al.*, 2003b, 2004). It seems this mimicking is more common in Norway and is probably an indirect effect of isolation, fragmentation and a shorter breeding season (due to the latitude), potentially effecting the chance of a conspecific tutor being found, especially for late hatchlings. It appears unlikely that the ortolan bunting male in its 2K year of life would sing only the yellowhammer-like songs if he also had ortolan bunting songs in his repertoire. This seems unlikely because yellowhammer-like songs do not induce responses from conspecific males (Osiejuk *et al.*, 2003b; personal observation). Thus, the appearance of such species-specific song types in the next seasons should be the result of learning new types during the first breeding season. Similar observations of probable learning later in life include new song types belonging to foreign dialects by males breeding at dialect borders (Cramp & Perrins, 1994).

Regardless of copying or inventing new syllables, repertoires could be enriched by the recombination of already possessed syllables into new sequences (e.g. in song sparrow, Podos *et al.*, 1992). Slabbekoorn, Jesse & Bell (2003) found that in island and mainland populations of white-crowned sparrow *Zonotrichia leucophrys nuttalli*, the song type variation among populations could be explained by the fact that dispersing males learn from multiple tutors and produce song type hybrids and that new song types emerge through the recombination of components from existing ones. Additionally, in the Savannah sparrow *Passerculus sandwichensis*, males have single song type repertoires and compose their song through drawing upon a set of model individuals (Wheelwright *et al.*, 2008). This learning process appears to be mediated by different mechanisms for different song parts, likely because they convey different information (Williams *et al.*, 2013). This was recently shown experimentally for both natal and first spring areas (Mennill *et al.*, 2018). Although the repertoire sizes of adult white-crowned and Savannah sparrows are extremely small, the processes suggested by Slabbekoorn *et al.* (2003) and Wheelwright *et al.* (2008) fit well with the pattern of song variation in ortolan buntings found in Norway (Osiejuk *et al.*, 2003a), where song diversity measured both at the individual and the population level is much higher than in stable populations in the central part of the distribution range. It has been shown for several ortolan bunting populations that virtually all males within a local dialect area share a relatively small number of song types with the same final structure (Cramp & Perrins, 1994; Łosak, 2007). In this light, because the Norwegian population has dozens of song types, large repertoire sizes, no common final song structure and individual males which have song types with different final structures, it seems to consist mainly of vocal hybrids (Osiejuk, Ratyńska, & Dale, 2007). The high fragmentation of the isolated population and an extensive dispersal pattern of males may explain why the ortolan bunting males from Norway are able to enrich and 'mix' their repertoire so much. The frequent changes in singing territories within and between breeding seasons related to failure in attracting females which are in short supply (Dale, 2001; Dale *et al.*, 2005, 2006) and resulted in frequent changes in social environment in terms of neighbours with different repertoires. This characteristic behaviour of the study population may be responsible for the observed pattern of repertoire changes, as males having settled in a particular group of neighbours trying to match their repertoires (Skierczyński, 2009). The recombination as a way of repertoire formation has also been stressed for the chaffinch *Fringilla coelebs*, where the recombination of sections from different song types was suggested as one of the mechanisms to achieve such a complex vocal output (Slater & Ince, 1979). This is also described in red-faced cisticola *Cisticola erythrops* males that have highly variable songs due to the improvisational recombination of shared syllable types (Benedict & Bowie, 2009).

Several studies of songbirds with small song type repertoires have revealed that young birds (usually in hatching-year summer) are able to acquire larger repertoires than are sung later in life. The process of selective attrition of song types that are not shared with later neighbours (white-crowned sparrow

Z. l. pugetensis Nelson, 2000, song sparrow *Melospiza melodia* Nordby, Campbell & Beecher, 2007) or not resembling the songs of neighbours (field sparrow *Spizella pusilla* Nelson, 1992) is responsible for a decrease of repertoire size, which thereafter remain stable for the rest of their lifetime. Similar selective attrition was observed in the ortolan buntings in Norway, as about 60% of longitudinally observed males lost some song types from their earlier repertoires. Interestingly, selective attrition was observed not only between 2K and 3K ages but also later, which could be linked to the fact that males in this population often change territories due to the lack of females. Consequently, attrition seems to take place not just once, but sequentially, as there is a necessity to adapt to new neighbours.

Unfortunately, there is no other long-term longitudinal data from other ortolan bunting populations allowing for a direct comparison of song repertoire changes in individuals. Thus, we cannot exclude the possibility that the unique song characteristics of the Norwegian population may be related to other factors than the ecological conditions suggested above. However, twenty years of research on a continuous and abundant population from Western Poland has revealed no age-related changes in repertoire size, contents or overall song diversity (e.g. Skierczyński & Osiejuk, 2010; Osiejuk, Bielecka & Skierczyński, 2012; Jakubowska & Osiejuk, 2018; own unpubl. data). The most important result of the present study is that under specific conditions a songbird species that typically possess a small and unchanging repertoire, across its life span, may considerably change the repertoire size and contents. We suggest that changes in population ecology due to isolation, fragmentation or conversely, expanding range, may considerably affect song behaviour. Analogously, one can expect that learned vocal traits in birds and other animal groups may also change quickly if something disturbs the learning process.

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