Song repertoires in a western European population of Yellowhammers Emberiza citrinella

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Abstract. Geographic variation is one of the most intensively studied bird song topics. However, our knowledge of geographical song variations in most species studied so far is very sparse, with many areas of the species-typical geographic distributions still unexplored. One striking example is the Yellowhammer: for this species most song studies have been conducted along well defined dialect borders, but almost nothing is known about its song characteristics in other regions of its broad geographic distribution. In this study, we investigated the song structure variations and stereotypes in different areas of western Belgium and northern France. We described 66 different song types (α-elements) in 45 males recorded. Each male had a unique individual repertoire consisting of 1 to 4 of these song types. This high variability at the individual level contrasted with the high homogeneity of the specific repertoire over the whole geographic distribution of the species. The evolutionary implications of such specificity are discussed with regard to song learning and timing of singing activity. Finally, all males recorded belonged to the western regiolect, although some mixed-singers were also recorded. These results contrast with the very few studies previously conducted in western Europe which have suggested that eastern regiolect songs were common in this geographic area.

Key words: Emberiza citrinella, Yellowhammer, song characteristics, recognition, dialect

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INTRODUCTION

Bird song is one of the most often investigated topics in behavioural biology. It is an excellent model for the study of complex social behaviours by virtue of its extensive variations both between and within species (Catchpole & Slater 1995, Kroodsma & Miller 1996). These variations led to decades of investigations on cultural learning and on behavioural and neural developments of these complex vocalizations that bear intriguing similarities with human speech (review in Ball & Hulse 1998). Bird song has two major roles: resource defence (e.g. territory) (Krebs 1977) and female attraction or stimulation (Kroodsma 1976), and variations in song potentially provide information about geographic origin, habitat, individual quality, motivation, sexual maturity, etc, information that are used during communication between conspecifics (Dhondt & Lambrechts 1992, Podos & Warren 2007).

Studies of European Bunting song focused mainly on the identification of traits that may be used in the contexts of individual, population and species recognition (Hansen 1978, 1985, Kreutzer 1979, Gailly 1982, Osiejuk & Ratynska 2003, Osiejuk et al. 2003). The Yellowhammer is probably the most common species of European Buntings, and for which the song has been described in more detail. This species has a short and stereotyped song (Fig. 1) composed of the repetition (part-A) of a sound complex, usually a double figure (α-element) assumed to be involved in individual recognition, and ending with one or two longer figures (part-B) that differ markedly between geographic regions (see Hansen 1985 for a description of the main end-part structures). Part-A has a typical crescendo volume, and incomplete songs are frequent and limited to this part of the song (Hansen 1978, but see Fig. 4 in Rutkowska-Guz & Osiejuk 2004). Each male possesses a repertoire of 1 to 4 (rarely 5) song types that

Former research mainly focused on aspects of geographic variation in Yellowhammer song, and described songs in regions where dialect barriers exist. These studies identified two major regiolects, one (often called *ty ziih*, *ty sieh* or *tee sii*) situated in the eastern part of Europe (Hansen 1985, Rutkowska-Guz & Osiejuk 2004), the other (often called *zi ty*) in the western part (Hiett & Catchpole 1982, Hansen 1985), with a barrier situated in Germany, and a mixture of regiolects also found in Denmark, northern Germany and Scandinavia (Hansen 1978, 1985, Möller 1982, Kaiser 1983, 1987, Glaubrecht 1989, 1991, Wonke & Wallischläger 2009). These two major regiolects have been subdivided in different minor regiolects: BC, BE, XsB and XlB (Wonke & Wallischläger 2009). Surprisingly, Yellowhammer song has been poorly described in western Europe, that makes further study needed, particularly because typical eastern regiolect songs have been recorded in France and in the United Kingdom (Hiett & Catchpole 1982, Cramp & Perrins 1993). Here we present the results of a detailed study of Yellowhammer song in a region belonging to the western regiolect that has never been sampled before. Our findings are discussed in the context of problems related to individual and dialectal discriminations.

**MATERIALS AND METHODS**

**Study areas and song recordings**

The study was carried out in 5 different areas situated in eastern Belgium (Condroz: 50°28’N–5°31’E; Famenne: 50°13’N–5°14’E; Ardennes: 50°24’N–6°08’E; Pays de Herve: 50°42’N–5°43’E) and northern France (French Lorraine: 49°05’N–5°35’E) (Fig. 2). These areas represent different kinds of landscapes that could possibly influence song structure.

Male Yellowhammers were recorded between February and June 2001 following the Altmann (1974) ad libitum method. Recording sessions started 1 hour before sunrise and continued during the morning, taking climatic conditions into account. The areas Condroz, Famenne and Pays de Herve were the most frequently visited. Birds were tape recorded along a well-defined transect established during the first visit. No attempt was made to map the territories. The recording equipment was a Sony Walkman Professional WM-D6C connected to a Sennheiser ME88/K6 directional microphone surrounded by an anti-wind shell.

**Song analyses**

All recordings were visualised and analysed with the PC software AVISOFT-SASLAB PRO v.3 (R. Specht, Berlin, 1995). The sonograms illustrated in the present paper were created using the SYRINX sound analysis program (v2.6h, John Burt, www.syrinxpc.com). The setup of the software was: sampling frequency: 44100 Hz, 16 bit, time resolution: 2.56 ms, FFT size: 512, Blackman window. During the study, 64 males were...
recorded and 620 sonograms from 45 individuals were analysed in detail (14 males in Condroz, 12 in Famenne, 5 in Ardennes, 7 in Pays de Herve, and 7 in French Lorraine). For the males recorded, 5 songs of each individual song type were analysed. Singing bouts analysed contained at least 40 songs per individual; we determined this threshold as the minimal sample necessary to register complete individual song repertoires. Samples with less than 40 songs were not considered in further analyses. This method is supposed to disclose all dialect (Møller 1982) and repertoire compositions (pers. obs.). On each sonogram, the following parameters were measured: duration and frequency range of each phrase and note, duration of songs and intervals.

In our study, song types were visually classified into groups and families, this classification was then confirmed with the more objective ID method (Bertram 1970). Thanks to an overlapping value, the ID method quantifies the differences (form, surface) between a note model drawn on a transparent millimetre grid and any other note or syllable printed on a sonogram (Fig. 3). Briefly, on a 1mm square tracing paper, a tracing is made round the outline of a sonogram of a given syllable (the model, Fig. 3a). The number of squares within the trace is counted. Note that in our study, we chose one a-element (composed of two notes, see Fig. 1) as a model instead of one single note as illustrated on the example on Fig. 3. The model chosen was one a-element of the most common song type in the population under study (illustrated on Fig. 4a). To compare the trace with any sonogram, the position of best fit (i.e. of greatest overlap) is found by eye, allowing unlimited freedom of movement of the trace along the time axis, and adjustment up to approximately 400Hz up or down the frequency axis. Fig. 3b shows the trace being compared with a sonogram of a different pattern. Each square of the 1mm square grid is assigned as "black" if it covers, at least partly, the syllable on the sonogram, or "white" if it does not cover the syllable considered. The degree of divergence (difference index: ID) is then obtained using the following formula: $ID = \frac{\text{number of black squares outside the trace}}{\text{total number of black squares}} + \frac{\text{number of white squares within the trace}}{\text{total number of squares within the trace}}$. In our example: $ID = \frac{43}{96} + \frac{42}{95} = 0.890$. The larger the ID the more different the syllables. In the classification, groups are made of similar sound complexes (song types) that only differ in fine details, whereas families are made of related groups of song types.

**RESULTS**

**A-elements at the population level**

In the 45 individual song repertoires analysed, a total of 102 song types belonging to 66 different a-elements were found (Fig. 4). These 66 different song types were compared and distributed in 21 different groups belonging to 12 families. A simple mathematical calculation, based on
a second-order polynomial regression and estimated from the number of new song types discovered along the analyses of individual song repertoires gave a total of 72 different song types. These 72 types would represent the maximal number of different song types that could be found in the geographical area under study (Fig. 5).

Among these 66 song types, 42 (79%) were unique, meaning that a large majority of them was sung by one male only (Fig. 6). The commonest song type was only produced by 10 individuals (a-elements “a” in Fig. 4). Thereafter, we compared the different a-elements found in our study with the different a-elements published in the literature of the Yellowhammer (Hansen 1981, 1984, 1985, 1999, Hiett & Catchpole 1982, Glaubrecht 1989, Rutkowska-Guz & Osiejuk 2004). From the 21 different groups of a-elements established in our study, 16 (72.2%) of them contained similar a-elements that were also found in the Yellowhammer literature.

A-elements at the individual level

Males sang between 1 (6 individuals) and 4 song types (2 individuals), with a majority of 2 types (24 males) and a mean individual repertoire size of 2.2 song types. Within individual repertoires, some song types were produced more frequently than others. Fig. 7 illustrates the relative abundance of the different song types of 6 males for which we had more than 100 songs recorded.

Geographic influence on song types and end-part structures

Comparing the 66 recorded song types across the recording areas did not reveal significant geographic variation, both at the level of song repertoire size (Kruskal Wallis test: $H_{(4,46)} = 4.338$, $p = 0.36$) and song type occurrence, tested for the 7 most widespread families separately ($\chi^2$ tests; $df = 4$, $p > 0.05$ in all cases). This means that the size of repertoire did not vary according to the considered region and that no regional grouping can be made in the composition of the individual repertoires.

Considering the end-part structures (part-B), the vast majority of songs belonged to the western regiolect (XlB form), that can be characterised by the interval between the end of the last a-element and the beginning of the last note of the song (Hansen 1985, Glaubrecht 1989) (see “i” in Fig. 1). In all western regiolect songs analysed here, this interval lasts at least 0.025 sec. However, among the 45 males used in our analyses, 4 had a song type in which this same interval duration was comprised between 0.006 and 0.020 sec (see example on Fig. 8). Such short intervals have been used

Fig. 5. Number of new a-elements (continuous trait) found during analyse of the individual repertoires. Analysis of the repertoires of 45 males revealed 66 different a-elements. The best model fitted to this analysis (dashed trait, equation shown on the figure) reaches a theoretical maximum of 72 different a-elements in this population.

Fig. 6. Frequency distribution of the different a-element types in the population under study ($N = 102$). Most a-elements are unique.

Fig. 7. Relative abundances of the different a-elements in the repertoires of six individual male Yellowhammers. Each bar represents one male, the different greyscales within each bar represent the different a-elements that composed the repertoire of each male. Similar greyscales between males do not necessarily mean that these males sang the same a-elements. Numbers within bars – number of songs analyzed.
to define eastern variants of the Yellowhammer song (forms XsB or B, see Hansen 1985, Glaubrecht 1989). Only one song type of the individual repertoires of the 4 males presented this part-B structure. Therefore, these males can be classified as mixed-singers, since both regiolect song structures were present in their repertoire (Wonke & Wallschläger 2009).

DISCUSSION

A-element structures

Song repertoires of 45 male Yellowhammers from different landscape areas in Belgium and northern France were analysed. We described 66 different a-elements (song types) that have been gathered in 21 groups and 12 families. The total specific repertoire of the Yellowhammer is estimated at 72 different song types. These results are extremely consistent with several previous studies made on this species in other European regions. In Denmark for example, the study of the same number of individual males gave a population repertoire size of 63 different song types (Hansen 1978). In another study in Denmark, Hansen (1999) estimated through a computer simulation based on a 175 male sample, that the theoretical specific repertoire should be of 80 different song types. Each male has an individual repertoire of 1 to 4 song types, with a mean value of 2.2. Other studies have found similar values of 2.05 (Hiett & Catchpole 1982), 2.1 (Hansen 1984, 1999) and 2.86 (Rutkowska-Guz & Osiejuk 2004). The high inter-individual variability in a-elements associated to the small overall individual repertoire sizes, is almost a guarantee for each male not to share the totality of its repertoire with another conspecific in the same area. We failed indeed to find two single males with the same repertoire composition, which seems to occur rarely in this species (Hansen 1981, Hiett & Catchpole 1982).

At the geographic level, the song types and the mean individual repertoire composition have a random distribution. No particular aggregation of a-elements or repertoire sizes have been found between areas. Moreover, there is a high similarity between the a-element structures described in Belgium and northern France with those published in the literature (Hansen 1981, 1984, 1985, 1999, Hiett & Catchpole 1982, Glaubrecht 1989, Rutkowska-Guz & Osiejuk 2004), which indicates that the general diversity of structures of the first part of the song is very homogenous at a macrogeographic level. This raises two major questions. Individual recognition. The high diversity of a-elements, and their organization in many different repertoire compositions, strongly suggest that this inter-individual variability represents a kind of fingerprint which may act as an individual recognition mechanism. Even if the birds studied here were not individually colour-ringed, it was often possible for the observer to identify each single male when combining the visual and acoustic information of territory positions and repertoire compositions (pers. obs.). In a previous study, Hansen (1984) showed that male Yellowhammers respond more strongly to stranger than to neighbour song repertoire, indicating that they can discriminate between familiar and unfamiliar song. However, no attempt was made to determine if the whole composition of the repertoire, the proportion of familiar song types, or any particular characteristic of the played song types were predominant in eliciting this aggressive reaction. This question is actually still open and needs further studies since individual recognition and recognition of familiar versus unfamiliar songs in birds may be based on a wide variety of song characteristics (Dhondt & Lambrecht 1992): repertoire composition, combination of song types within the repertoire, combination of song characteristics and song post location (Lovell & Lein 2005), precise rendition of each song type or note, and voices characteristics (but see Weary & Krebs 1992, Beecher et al. 1994). In the Reed Bunting Emberiza schoeniclus, a related species of the Yellowhammer, the individual recognition seems to be enclosed in the fine structure of the first note of the song (Gailly 1982). Recently, Skierczynski et al. (2007) have shown that a single song type, extracted from individual repertoires, was sufficient for Ortolan Bunting Emberiza hortulana neighbour-stranger discrimination;
suggesting that repertoire composition per se is not the main recognition process in this particular species.

On the other hand, several studies have shown that a high level of type sharing between neighbours may compromise individual recognition (McGregor & Avery 1986), at least temporally (Stoddard et al. 1992, Beecher et al. 1994). In the present study, due to the high diversity of repertoire compositions, very few sharing was recorded, and this never concerned more than one song type (pers. obs.).

**Species recognition and cultural transmission.**

The comparison of the structure and composition of the first part of the Belgian Yellowhammer song with other geographic areas where it has been investigated revealed many similarities. Moreover, it has been shown that the structure of the song types in a population was stable for decades, with an annual survival for each song type estimated at 95% (Hansen 1999). This kind of highly stereotyped global song structure is also a characteristic of many other Emberizidae species, and is often considered as a key element in the species recognition. But the most interesting question is how could such a high local variability in the song types occur in parallel with a high similarity of the species repertoire on the whole geographic distribution of the species? One possibility is that the learned song repertoire should be much larger than the effective repertoire that each male will produce (Thorpe 1958, Nottebohm 1975, Geberzahn & Hultsch 2003). This question is not solved yet, but there is some evidence for a large learned repertoire size in Yellowhammer since several males have been heard singing uncritically song with a high number of different structures in early spring (pers. obs.). This was also described by Rutkowska & Osiejuk (2004), who recorded a male in Poland singing 8 different song types. In both case, this never happened again later in the reproductive season. To learn and recognize a significant part of the species repertoire, each male should be, early in life, in contact with many different singing males. This could be a possible explanation for the extremely late singing and long lasting activity of the Yellowhammer during the time course of the breeding season (Rollin 1958, Hiett & Catchpole 1982). Large patterns of dispersal after fledging, preference for settlement in areas where song type repertoires are different from its own repertoire, selection of the memorised song models that are rarer in the settling area, and/or large diversity of bird origins in the composition of the winter flocks are other mechanisms by which song type diversity might spread over the geographic distribution of the species.

Another interesting and alarming point would be to look how the species repertoire of the Yellowhammer will evolve in the next decades since the population effective and densities are reducing in many different areas (e.g. Siriwardena et al. 1998) and sometimes face a significant reduction of genetic diversity (Lee et al. 2001).

**End-part structures**

All Yellowhammer males recorded in this study sang terminal whistles from the western dialect, corresponding to the XlB form (Hansen 1985). However, four males where recorded with mixed end-part structures; their repertoires containing both XlB and XsB or XB whistle figures. This result is consistent with the findings of Wonke & Wallischläger (2009) that XsB figures only occurred in males also singing the XB dialect (mixed-singers), and may somewhat question the real dialectal character of this particular end-part structure. The presence of typical eastern end-part structures in western regions has already been debated. Hiett & Catchpole (1982) and J-C Roché (in Cramp & Perrins 1993) found eastern typical song structures in western Germany, England and France, regions supposed to be enclosed in the western dialect area. However, in contrast to Hiett & Catchpole (1982), the occurrence of the eastern end-part structure in this study was extremely low, and only concerned males who also had western end-part structures in their repertoire. Such a rare phenomenon may be attributed to song copying errors. However, one would expect copying error mechanisms to create novelties (Podos & Warren 2007), which was not the case here. Alternatively, the occurrence of the eastern end-part structure may be restricted to males born in the vicinity of a dialect border. These males might have been in contact early in life with singing males from both dialect areas (Hansen 1978, Möller 1982, Glaubrecht 1989, 1991). This hypothesis further supports large dispersal patterns of young Yellowhammers. Individual leg-banding, chemical analyses of stable isotopes, or genetic analyses are now making possible to determine the geographic origin of individual birds (Webster et al. 2002). Some of these techniques are relatively recent and may be relevant tools to understand the occurrence of local rare song structures.
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STRESZCZENIE

[Repertuary śpiewu w zachodnioeuropejskiej populacji trznadla]

Zmiennieść geograficzna to jeden z najczęściej badanych aspektów zmienności śpiewu ptaków. Mimo to wiedza o niej jest wciąż niepełna i fragmentarycznie rozrzucona po różnych taksonach. Szereg specyficznych gatunkowo
właściwości zmienności geograficznej nie doczeekało się szczegółowych badań. Trznadel należy właśnie do takich gatunków, ponieważ dotychczasowe badania dotyczyły głównie makrodialektami (ang. regiolects) rozcierańymi się na dużych obszarach, a w szczególności wykrycia granic między nimi. Wiadomo, że makrodialekty u trznadla różnią się głównie strukturą końcowych gwizdów w śpiewie (Fig. 1), które są specyficzne dla makrodialektu i współdzielone przez większość samców na danym obszarze. Niewiele natomiast wiadomo czy jakie wzorce zmienności śpiewu występują wewnątrz takich jednolitych obszarów. W niniejszych badaniach skupiono się na zmienności struktury śpiewu i stereotypowości jego wykonania na terenie zachodniej Belgii i północnej Francji. Nagrano 45 samców z 5 różnych lokalizacji (Fig. 2), u których wyróżniono 66 różnych typów śpiewu na podstawie struktury tzw. elementu a, czyli sylaby tworzącej tryl pierwszej części piosenki (Fig. 1). Każdy samiec posiadał unikalny repertuar składający się z 1–4 różnych typów śpiewu, największa grupa osobników (24 samce) używała 2 różnych typów śpiewu, a średnia wielkość repertuaru wyniosła 2.2. Dokładna analiza nagrań 6 samców dla których zarejestrowano ponad 100 piosenek, pokazała, że nawet w przypadku repertuarów większych niż 2, samce najczęściej wykonywały 2 typy piosenek (Fig. 7). Większość z nagranych typów śpiewów (79%) była unikalna, tj. śpiewana przez dokładnie jednego samca z analizowanej próby (Fig. 6), a najczęstszy typ śpiewu (a-element typu „a”, Fig. 4) wykonywany był przez 10 samców. Zaobserwowano więc wysoką zmienność indywidualną repertuarów, która kontrastowała ze stosunkowo niewielką zmiennością na poziomie całego obszaru geograficznego objętego badaniem. Nie stwierdzono istotnych statystycznie różnic w wielkości repertuarów czy ich składzie między 5 badanymi lokalizacjami. Prawie wszystkie nagrane samce śpiewały piosenki należące do zachodniego makrodialektu, zaledwie cztery osobniki posiadały w swoich repertuarach piosenki wykazujące cechy mieszane, świadczące od podobieństwie do makrodialektu wschodnioeuropejskiego (Fig. 8). Specyfika zmienności geograficznej śpiewu trznadla została przedyskutowana w odniesieniu do procesu nauki śpiewu oraz czasu aktywności głosowej samców u tego gatunku. Zaobserwowany wzorzec zmienności przestrzennej śpiewu trznadła wskazuje na potencjonalną rolę zmienności osobniczej repertuarów w rozpoznawaniu indywidualnym, bowiem sąsiadujące samce mają najczęściej odmienne repertuary. Z kolei podobieństwo struktury końcowej frazy dialektowej na dużych obszarach wskazuje, iż młode ptaki mogą osiedlać się daleko od miejsca wylęgu, pozostając wciąż w obrębie własnego makrodialektu, gdzie mogą wchodzić w interakcje terytorialne z innymi osobnikami. Niemniej sugestie dotyczące wzorców dyspersji należy potwierdzić badaniami z użyciem odpowiednich metod genetycznych bądż stabilnych izotopów.