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Territorial reactions of male Yellowhammers (*Emberiza citrinella*) toward a specific song structure

Thibaud Gruber · Laurent Nagle

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Abstract Male songbirds assess their rivals by listening to their songs and, in some species, are especially sensitive to certain parts of the song. Yellowhammers (*Emberiza citrinella*) sing songs with different structures consisting of an initial phrase of stereotyped and repeated notes in a trill, and a terminal phrase, present or not, which consists of low or high frequency whistles that we called elements. We analyzed 1,055 songs from 25 different males and found that four different structures could be distinguished in a French Yellowhammer population. We found that the frequency ranges of the elements were more constant across individuals than the ranges of the notes, and among them, the low frequency element was nearly twice as conserved as the high frequency element. Then, in the wild, we tested the territorial responses of males to the four different structures and found that the full song structure, which is composed of the initial phrase followed by a high frequency element and a low frequency element, induced stronger territory defence responses from the males than any of the other structures. As only the structure containing the initial phrase and the low frequency element also induced a strong response, we propose that the main element responsible for the enhanced reaction of the males is

the low frequency element, which is consistent with the fact that it is more conserved than the other constituents.

Keywords *Emberiza citrinella* · Song structure · Territory defence · Yellowhammer

Introduction

Male passerine songs are believed to have two functions in sexual selection: territory defence and mate attraction (Catchpole and Slater 1995). Their songs are more or less complex in their structure and composition, and repertoire sizes also vary according to the species (Marler 1997; Todt and Hultsch 1996). It has been suggested that, depending on the species, either the choice of song type (Luschi and del Seppia 1996) or the song pattern (Beecher et al. 2000; Rutkowska-Guz and Osiejuk 2004) could have a specific function. It has also been shown that some elements of a song are directly responsible for a specific response from birds, notably in males (Nagle and Couroux 2000; Rehsteiner et al. 1998). Passerines may vary their song structure according to the intended audience: depending on the species, long, complex, and variable songs appear to be used for mate attraction, while short, repeated, and stereotyped songs seem mostly aimed at other males (Catchpole 1980, 1981; Krebs 1977; Slater 1981).

Yellowhammers (*Emberiza citrinella*) possess both structures in their songs: an initial phrase, composed of repeated syllables of one or two notes, and a terminal phrase, composed of one or two whistles (which we will here refer to as elements) which are not always present (Hansen 1978). The different song structures produced by the males are also produced at different rates (Hiatt and Catchpole 1982). Finally, this species is characterized by a

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small repertoire of 1–4 song types (Hansen 1984; Hielt and Catchpole 1982; Osiejuk 2001; Rutkowska-Guz and Osiejuk 2004). Given the different singing features found in this species, and following previous work by Rutkowska-Guz and Osiejuk (2004), we presumed as a preliminary hypothesis that any meaningful signal would most likely be found in the structural variation of the song itself rather than in the song type choice.

The aim of this study was to assess the existence of song structure specificity in male Yellowhammers in a territory defence context. More precisely, we wanted to know if any of the structures that can naturally be found in Yellowhammer songs was more likely to induce a territorial answer from another male Yellowhammer. It has been shown that male birds extract information from vocal interaction to assess rivals (Mennill and Ratcliffe 2004; Naguib et al. 1999; Peake et al. 2001), so we expected the males to react differently to the different structures, for instance, if one particular structure presented a particular threat to them. The song structures in Yellowhammer differ the most in their terminal phrase, especially by the presence or not of a low frequency element (Hansen 1978). Its presence allows us to discriminate easily between the song structures, making the song longer and more complicated, we hypothesized that it would constitute a key feature to take into account for the males.

Firstly, we analyzed the songs of a French Yellowhammer population to characterize their singing pattern, which differs among geographic areas (Hielt and Catchpole 1982). Then, we conducted a playback experiment on the same population, during which we recorded several territorial reactions—i.e., latency and distance of approach to the loudspeaker and time spent in the vicinity of the loudspeaker (Brooks and Falls 1975)—to the four different song structures that had been characterized with the previous analysis. Finally, we compared these territorial responses to the four structures in order to determine if a particular structure or a certain element it contained induced an enhanced territorial response.

Methods

Subjects and study area

The study was carried out in the municipality of Lassigny, Oise, Picardie, France (coordinates of the center of the study area, Lagny: 49°37'N, 2°55'E). Playback experiments were conducted on 19 male Yellowhammers, a species commonly found in this region along forest edges and in tree lines surrounded by farmland. Males were found in territories identified by one of the authors (L.N.). Each male was tested with the songs of a distant male

whose territory was far enough from its own territory so that this bird would not be possibly heard, thereby avoiding any neighborhood effect. Moreover, the latter male was chosen so that his song would not overlap with the tested male's repertoire to provide a new stimulus. For all the subjects, songs were recorded before and after the playback, in order to make sure that the song used to test him was not part of his repertoire, as well as to check that the same male was tested on two consecutive days of testing, as these birds were not banded. Playbacks were conducted between 10 April and 5 May 2007, during the breeding period (Peakall 1960). No significant difference in the Yellowhammers' responses, either vocally or behaviorally, was found between April and May, independently of whether the experiment was conducted in April or May.

Song structure and terminology

Yellowhammer songs have two distinct parts (Hansen 1978) which have been named initial phrase and terminal phrase (Hielt and Catchpole 1982). The initial phrase is the repetition of one or two notes (which are called syllables). The variety of this initial segment is referred to by the song type (Hansen 1978). The terminal phrase can contain either a high frequency element or a low frequency element or both. Following Hielt and Catchpole's terminology (1982) we named:

- *No terminal phrase* (NTP, Fig. 1a): the structure where only the initial phrase is present.
- *No high frequency element* (NHE, Fig. 1b): the structure where the initial phrase is followed by a terminal phrase constituted only of the low frequency element.
- *No low frequency element* (NLE, Fig. 1c): we created and named this new category for a structure that was found in the French studied population but was not present in Hielt and Catchpole (1982). We chose this name because it contains the initial phrase followed by a terminal phrase comprised only of the high frequency element.
- *Full song structure* (FSS, Fig. 1d): the structure where the initial phrase is followed by a terminal phrase constituted of both the high frequency and the low frequency elements.

Additionally, we found that the high frequency element could be found either in a short version or a longer version (Fig. 2) whereas the low frequency element is always long. Finally the nature of the high frequency element was not found to be linked with the song type: we found that this high frequency element could be found in either a long form or a short form in a same song type, and even produced by the same bird.

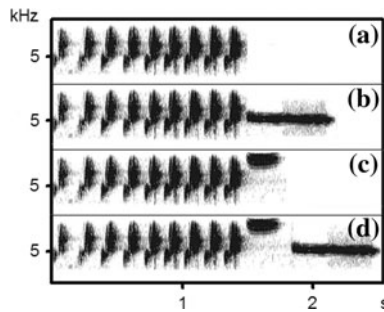


Fig. 1 Sonograms of Yellowhammer (*Emberiza citrinella*) song showing the four different structures that were found in the studied population. *a* No terminal phrase (NTP) where only the initial phrase is present, *b* no high frequency element (NHE) where the initial phrase is followed by a low frequency element only, *c* no low frequency element (NLE) where the initial phrase is followed by a high frequency element only, *d* full song structure (FSS) where the initial phrase is followed both by high and low frequency elements. NTP, NHE and NLE were built from FSS structure, using Avisoft SASLab Pro 2 and Audacity programs

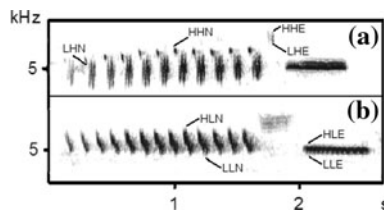


Fig. 2 Sonograms of Yellowhammer songs showing the two different high frequency elements that were found in the studied population and the measured frequencies. *a* Short high frequency element shown in a full song structure. *b* Long high frequency element shown in a full song structure. Both sonograms were made using Avisoft SASLab Pro 2. *HHN* High frequency of high frequency note. *LHN* Low frequency of high frequency note. *HLN* High frequency of low frequency note. *LLN* Low frequency of low frequency note. *HHE* High frequency of high frequency element. *LHE* Low frequency of high frequency element. *HLE* High frequency of low frequency element. *LLE* Low frequency of low frequency element

Song analysis and playback stimuli

Stimuli were created from songs of 25 males of the same population recorded between 22 March and 8 June 2006 and during two periods of the day: between 0700 and 1200 and between 1625 and 1945 hours, respectively (UTC + 1). Birds were recorded with a Telinga Pro 6 Phantom parabola and microphone and a Nagra Ares-BB + digital recorder. Songs were firstly analyzed using Avisoft SASLab Pro 2 (for download of newest versions, http://www.avisoft.com/download_.htm). A total of 1,055 songs were analyzed, with a mean number \pm standard deviation (SD) of 40.3 ± 29.7 songs per male. Length, type, frequency ranges, and structure were measured for each song. Song abruptions were not taken into account

during the analysis. Minimum and maximum song and interval duration were calculated according to Naguib and Kipper's (2006) method. To generate stimuli, we selected 19 different full song structures (FSS) from 19 different males that we edited in order to obtain the four structures described previously (see Fig. 1) using Avisoft SASLab Pro 2. These 19 song structures were selected to test the highest possible number of song types with the highest possible number of singers. Each selected song thus differed from the others by its singer to avoid pseudoreplication (Kroodsma 1986). Moreover, 17 of them differed by their song type. The two remaining selected songs were of two previously used types, but sung by a different singer and with a different high frequency element than found in the first one: i.e., with a long high frequency element or a short high frequency element, depending on the singer (Fig. 2). As short and long high frequency elements were found at the same rate during the analysis of the 25 males' song types, we selected 9 "short high frequency element" types and 10 "long high frequency element" types. Previous analyses of Yellowhammer songs based on the recordings for the 25 males (for a total length of 3 h 50 min) indicated that the mean inter-song interval within a bout was of 7.93 ± 1.52 s and the mean song duration was of 2.05 ± 0.31 s. Therefore, we built sequences of one song from one male and with a given structure (FSS, NHE, NLE, or NTP) followed by the length of silence required to make up a total of 10 s. This sequence was repeated 30 times in order to build a 5-min stimulus. In summary, the stimuli consisted of 17 song types plus 2 types already used but with a different high frequency element, all sung by different males. Each one was presented to a single male who was only exposed to this type, but within the four different structures (FSS, NHE, NLE, and NTP) edited from the initial FSS. All the stimuli were normalized via Audacity to the same amplitude.

Playback protocol

Playback experiments were conducted between 0710 and 1354 hours, between 10 April and 5 May 2007, on 19 males found in the field. Whenever a male was found singing in his territory, we installed a Elipson C10 AL loudspeaker on a hypothetical line drawn between two posts he had been observed singing from, 10 m from one of the two spots. We delimited a 10-m diameter around this spot that we called the zone. This installation did not result in much stress for the bird that either stayed where it was or moved nearby and started singing again. Hearing the bird was a confirmation of its presence nearby so that we could make sure it was still in its territory and would hear the playback. We considered that it did also provide a way to control the proximity to the zone (and therefore, their

possibility to reach the zone as soon as possible) for all the birds at the start of the experiment, a parameter which may otherwise have interfered with the latency analysis. As soon as the installation was completed, we began the broadcast of one group of stimuli (4 structures from the same song type) from a database built in an Archos Gmini XS100 MP3 Player in WAV file format. The MP3 player and the speaker had been previously adjusted to play the songs with a power of 80 dB at 1 m distance. A 5-min stimulus from a single song type was played to the subjects, followed by a 15-min break, before receiving another 5-min stimulus from the same type but with a different structure. The same protocol was used on the same male the following day, during the same period of the day, with the two remaining structures to be tested to conduct the playback in the same environmental conditions. Structure order during the broadcast was randomized for each male.

For each session (i.e., a sequence of 30 repetitions of the same stimulus), we measured three different variables:

- *Latency*: delay between the beginning of the playback and the arrival of the male inside the zone;
- *Duration*: time the male spent inside the zone;
- *Distance* to the loudspeaker: the closest distance to the loudspeaker where the bird alighted.

Statistical analysis

An analysis of variance (ANOVA) was conducted to assess if the order of play and the structures had an effect on the birds' answer, i.e., if they approached the loudspeaker or not. A Friedman test was used to compare the distribution of structures according to song types. We analyzed the distribution of values for each tested variable (latency, duration, distance) with a multivariate general linear model (MGLM), followed by pairwise multiple comparison procedures (Student–Newman–Keuls method) to compare each structure with the others. All the birds were present in their territory and heard by the experimenters at the start of the playback and reacted to at least one structure. We used a Levene test to assess the equality of variances between song frequency ranges. Therefore, we could assess the consistency of the frequency of components of the song among individuals. A Wilcoxon test was used to compare males' responses to the nature (short or long) of the high frequency element. Finally an ANOVA with repeated measures was used to assess the impact of high frequency element (short or long) propagation on males' responses. To conduct these analyses, we used SigmaStat program (Systat Software, San Jose, CA, USA) and SPSS for Windows Release 8.0.0 (22 December 1997) Standard version (SPSS, Chicago, IL, USA).

Results

Analysis of the French Yellowhammer population's song characteristics: four song structures and small repertoire size

1,055 songs from 25 different males (mean number of 40.3 ± 29.7 songs per male) recorded the year before the playback experiment (22 March–8 June 2006) were analyzed to characterize the population: the mean size of the repertoire was 1.96 ± 0.73 song types and repertoires varied from 1 to 4 song types. Song types were sorted according to visual and acoustic properties (frequency ranges and number of notes) from rough WAV recording files analyzed with Avisoft SASLab Pro 2. We found a total of 23 different song types with either 1 or 2 repeated notes in the initial phrase. Four out of 23 types contained one repeated note in their initial phrase (13%) while 19 contained two repeated notes (87%). Concerning the terminal phrase, 8 out of 23 types were found with a long high frequency element only (35%), 9 types were found with a short high frequency element only (39%), and 4 types were found with both long and short high frequency element but in different males (17%). Two types were not found with a final high frequency element (9%). Four different song structures were found: NTP (no terminal phrase), NHE (no high frequency element), NLE (no low frequency element), and FSS (full song structure). FSS was the most represented structure in the population (64.4%), followed by the NTP structure (23.3%), and finally NLE (10.1%) and NHE (2.2%) (Table 1). Both analysis by male and by song type showed that FSS was the most common structure that could be found in the population: 23 males out of 25 (92%) presented this structure at least for one type, and 19 song types out of 23 (82%) were recorded with this structure (Table 1). Even though only 1 male (4%) was recorded with the four different structures, 18 out of 25 presented at least three different structures (including FSS). Furthermore, 2 out of 23 types were recorded with the four structures, but 13 out of 23 (56%) were recorded at least with three different structures (including FSS).

Song type selection has no influence on the composition of the terminal phrase of the song

Inside each of the 23 song types, we counted the number of exemplars of each structure (NTP, NHE, NLE, and FSS) that could be found for the song type in the recorded files. A Friedman test showed that the song type had no significant influence on the composition of the terminal phrase ($X^2_{21} = 25.226$, $P = 0.238$). Song type selection is therefore not responsible for the terminal phrase choice and

Table 1 Song count and proportion of the different song structures found in a population of 25 French male Yellowhammers (*Emberiza citrinella*) presenting 23 different song types

Song structure	Song count	%	No. of males ^a	% ^b	No. of song types ^a	% ^b
Full song structure	679	64.4	23	92	19	82
No low element	107	10.1	18	72	15	65
No high element	23	2.2	6	24	5	22
No terminal phrase	246	23.3	22	88	18	78
Total	1,055	100				

^a Number of males (and song types) observed with the song structure

^b Corresponding percentage relative to the total number of males (25) and song types (23)

Table 2 Basic song parameters of the studied French Yellowhammer population, based on 25 males

Variable	Number of songs	Mean ± SD	Minimum	Maximum
Song duration (s)	1,048	2.05 ± 0.31	1.73	2.36
Interval duration (s)	1,022	7.93 ± 1.52	6.40	9.45
Repetition (<i>n</i>)	1,048	10.35 ± 1.76	5	17
High high note (kHz)	1,043	7.23 ± 0.53	5.68	8.52
Low high note (kHz)	1,043	4.67 ± 0.48	2.92	6.45
High low note (kHz)	1,048	5.73 ± 0.68	3.44	8.69
Low low note (kHz)	1,048	3.73 ± 0.55	2.06	7.32
High high element (kHz)	1,033	8.76 ± 0.26	6.35	9.64
Low high element (kHz)	1,033	7.03 ± 0.31	5.42	9.04
High low element (kHz)	1,028	5.87 ± 0.25	4.99	6.71
Low low element (kHz)	1,028	4.33 ± 0.17	3.61	5.08

males can finish their songs (no terminal phrase, one or two final elements) independently of the song type.

Basic songs parameters and conservation of the final element in population

The analysis of the 1,055 songs allowed us to draw out the basic song parameters of the studied population, and to build the playback stimuli as close as possible to the mean ranges (Table 2). Mean song duration (2.05 ± 0.31 s) and interval duration (7.93 ± 1.52 s) combined to make a unit roughly 10 s in duration that was repeated 30 times to build one stimulus sequence as described in “Methods”. The mean number of repetitions of the note in the initial phrase (10.35 ± 1.76) was also taken into account to build the stimuli.

For each song, we measured the high and low extreme frequencies of both notes (the repeated, stereotyped constituents of the initial phrase) and elements (the two possible constituents of the terminal phrase) (see Fig. 2). Mean ranges were determined for the four different constituents: low frequency note (LN), high frequency note (HN), low frequency element (LE), and high frequency element (HE)

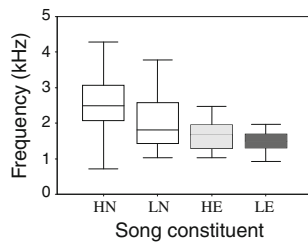
(Table 3). In order to assess whether the variation around the mean range was significantly different between notes and elements, we used a Levene test to assess the homoscedasticity of the ranges. We found that the standard deviations around the mean were not significantly different between HN and LN ($P = 0.88$), but were significantly different between LN and HE ($P = 0.007$), and between LE and HE ($P = 0.008$). In conclusion, the standard deviation around the mean range of the low frequency element is significantly smaller (1.75 as small) than the standard deviation around the mean range of the high frequency element, which is itself significantly smaller (1.7 as small) than the standard deviations of either high or low frequency notes (Fig. 3).

Latency and distance variables depend on the song structure during playback experiment

Birds reacted similarly to the different stimuli during playback, independently of their moment of broadcasting (first or second during the first or the second day of playback): 15 males out of 19 reacted to the first stimuli played and 14 out of 19 reacted to the second stimuli during the first day of

Table 3 Mean frequency ranges and associated standard deviations found for notes and elements in a French Yellowhammer population

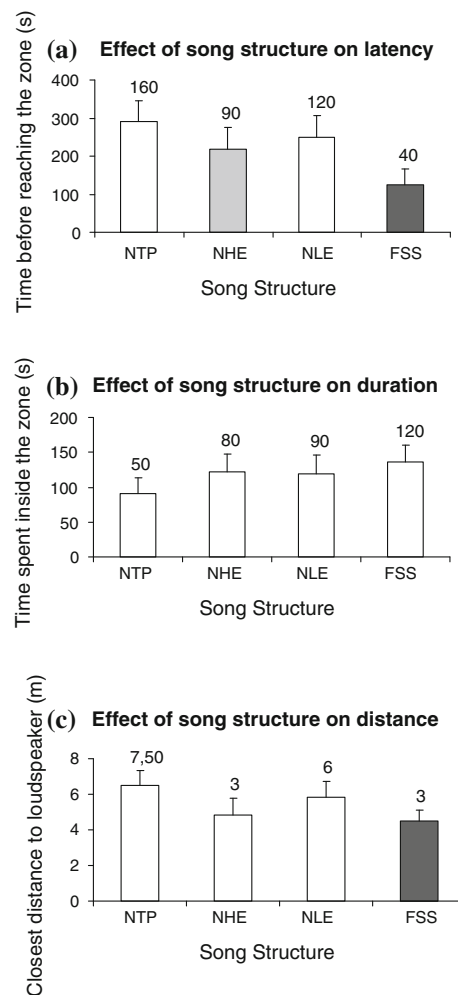
Variable	Minimum	Maximum	Mean	Standard deviation	Coefficient of variation
High note (kHz)	0.71	4.29	2.60	0.81	0.31
Low note (kHz)	1.04	3.78	2.00	0.81	0.40
High element (kHz)	0.82	2.48	1.62	0.47	0.27
Low element (kHz)	0.25	1.96	1.49	0.27	0.18

**Fig. 3** Box plots presenting the distributions of frequencies of the four main constituents of the Yellowhammer song in a French population: high frequency note (HN), low frequency note (LN), high frequency element (HE), and low frequency element (LE)

testing, while 13 males out of 19 reacted to the first stimuli and 14 out of 19 reacted to the second stimuli the second day. It also appears that the selected protocol based on two tests per day during 2 days did not affect the birds' responses to the playback: they reacted actively to the stimuli in all cases, independently of when they were broadcast either on the first day or the second, first or second in order (ANOVA, $F_{3,72} = 0.16$, $P = 0.923$) and independently of the structure that was broadcast (ANOVA, $F_{3,72} = 1.459$, $P = 0.235$). No interaction was found between the two parameters. Overall, 7 birds did not react to NTP (4 in first series, 3 in second series), 6 birds did not react to NLE (3 in first series, 3 in second series), 5 birds did not react to NHE (3 in first series, 2 in second series), and only 2 birds did not react to FSS (both in second series). 9 birds reacted to all the structures proposed.

Latency

The distribution of the latencies showed that they differed significantly (MGLM, $F_{3,72} = 7.034$, $P < 0.001$) according to the song type (NTP, NHE, NLE, FSS). Pairwise multiple comparisons showed that most of the latency reactions were different from each other when compared pairwise. NLE and NTP were not significantly different: NLE versus NTP: $q = 1.001$, $P > 0.05$, but NHE and NLE were significantly different: NHE versus NLE: $q = 4.294$, $P < 0.05$, and NHE and FSS were significantly different: FSS versus NHE: $q = 4.717$, $P < 0.05$ (Fig. 4a).

**Fig. 4** Reactions of male Yellowhammers to no terminal phrase (NTP), no high frequency element (NHE), no low frequency element (NLE), and full song structure (FSS) song structures playback. **a** Effect of song structure on latency reaction during the playback. **b** Effect of song structure on duration inside the zone during playback. **c** Effect of song structure on distance to loudspeaker during playback. All data are shown as function of song structure, with standard error. Mean values represent responses to song structures and are illustrative only as all statistics were non-parametric. Median value is given above each mean. Significant differences in multiple pairwise comparisons with all the other structures are presented in *different colors*. No significant differences in multiple pairwise comparisons are presented in the *same color*

Duration

The distribution of the durations inside the zone showed no significant differences between structures (MGLM, $F_{3,72} = 2.404$, $P = 0.074$; Fig. 4b).

Distance

The distribution of the distances showed that they differed significantly (MGLM, $F_{3,72} = 4.765$, $P = 0.004$) according to the song type (NTP, NHE, NLE, FSS). The pairwise multiple comparisons showed a significant difference when FSS was compared with all the other structures: FSS versus NTP: $q = 4.384$, $P < 0.05$, FSS versus NLE: $q = 4.077$, $P < 0.05$, FSS versus NHE: $q = 4.48$, $P < 0.05$. Other structures compared pairwise showed no significant differences for this parameter: NTP versus NHE: $q = 2.833$, NTP versus NLE: $q = 2.622$, NHE versus NLE: $q = 1.610$ (Fig. 4c).

The nature of the high frequency element has no effect on the male Yellowhammer's response

When comparing the responses of males to a short (s , $n = 9$) or a long (l , $n = 10$) high frequency element in the no low frequency element (NLE) structure, we did not find any significant difference for any of the tested variables: latency (Mann–Whitney U test: $U = 37.5$, $N_1 = 9$, $N_2 = 10$, $P = 0.549$), duration (Mann–Whitney U test: $U = 36$, $N_1 = 9$, $N_2 = 10$, $P = 0.497$) or distance (Mann–Whitney U test: $U = 36.5$, $N_1 = 9$, $N_2 = 10$, $P = 0.497$).

Moreover, when comparing latency responses between NLE structures and their corresponding NTP structure (NLEs with corresponding NTPs and NLEl with corresponding NTPl), no interaction was found between the nature of the high frequency element and the effect of the structure (ANOVA with repeated measures, no effect was found for the structure: $F_{1,17} = 1.14$, $P = 0.301$, nor for the high frequency element length: $F_{1,17} = 0.996$, $P = 0.332$, and no interaction between structure and high frequency element length was found: $F_{1,17} = 0.037$, $P = 0.85$). In summary, the difference in latency response between NLEl and NTPl was not significantly different from the difference between NLEs and NTPs.

Discussion

In this study, we have shown that in Yellowhammers, the full song structure (FSS) elicits more territorial reactions from males than the three other structures that are found in the studied population. Even though the birds reacted similarly to any species-specific stimuli broadcast suggesting

that a male was intruding their territory, they reacted more strongly in the case of the FSS structure. The fact that birds reacted equally to all types of structures is explained by the fact they considered any intrusion a threat and therefore went to look for the intruder; however, the degree of intensity they showed in their answer depended on the structure that was broadcast. There were significant structure effects for both the latency of responses and the distance to the loudspeaker: males whose territory was being intruded upon reacted faster and came closer to the emission source when the FSS was broadcast than they did for the other structures. There were no significant differences in the duration of the stay of males inside the 10-m zone around the loudspeaker. This variable may not have been appropriate for this protocol. A better indicator of the male's motivation may be the duration of stay during and after the playback, possibly the time birds would wait after the opponent has left to ensure he does not return. However, only a few males out of the 19 tested stayed in the zone until the end of the test, regardless of the structure that was broadcast. A possible explanation is that when the birds arrived in the zone and did not find another male Yellowhammer, they became disinterested in the playback, whatever its structure, and left the zone.

Both latency and distance to the loudspeaker were found to be respectively shorter and smaller when FSS was broadcast, and the latency found when NHE was broadcast was also significantly smaller than when NLE or NTP were broadcast. Although not significantly different from the values found for NLE and NTP, the mean distance value found for NHE is smaller than the mean values found for NLE and NTP, so that we can form the hypothesis that the main element which is responsible for the male reaction in the FSS is the low frequency element. This hypothesis is supported by the fact that FSS is not found in some Yellowhammer populations where NHE can be found (Hansen 1978; Kaiser 1965).

Two questions can be raised from our results: is the low frequency element directly responsible for the Yellowhammer reaction, or is it the duration of the FSS which is responsible for the enhanced reaction observed by males, and in this case, would the nature of the low frequency element be purely epiphenomenal with this exaggerated reaction?

Both duration and propagation of the different songs are affected by their composition: a longer song like an FSS song could thus elicit more reactions than a shorter song like an NTP song. If duration was the only characteristic assessed by males (so that a longer song would provoke an enhanced reaction), we would have obtained significantly different results for the NLE songs, depending on whether they had a long or a short high frequency element. No significant difference was found between these two

“sub-structures”. Moreover, the high frequency element can be found either in a long form or a short form, which constitute two groups in our data: NLEs (for the song type with a short high frequency element) and NLEl (for the song type with a long high frequency element). The comparison of the relative difference between the paired NTP and NLE structures also supports the claim that duration is not a sufficient factor to explain the enhanced reaction from the birds. If duration was the most important factor taken into account by birds, their reactions to NLE structures relatively to the paired NTP structure should be stronger if the NLE contains a long high element rather than a short high element, as the long high element is longer than the short high element. We did not observe any significant differences between the two situations, therefore making it unlikely that duration is the only factor driving the birds’ reactions. Concerning propagation, FSS is composed of trills and whistles, and it has been suggested in the literature that whistles have better long-range transmission (Slabbekoorn et al. 2002; Wiley and Richards 1982) than broadband trills (Naguib 2003), and signal degradation is also thought to affect song recognition (Naguib et al. 2000). Therefore, FSS songs should be heard more easily because of less signal degradation and better propagation. However, NLE structures also contain the high frequency element, which is a whistle, and its propagation properties should then also increase the males’ reaction, compared with the reaction to the NTP structure. As for duration, if propagation alone was responsible for bird attraction, NLEl should be more attractive in relation to its NTPl version than NLEs to its respective NTPs version, because of a difference of length and propagation; Slabbekoorn et al. (2002), indeed, suggested that the longer the whistle, the bigger the behavioral response. The differences between NLEl and NTPl on the one hand, and between NLEs and NTPs on the other hand, are not significantly different, indicating that the propagation and length properties of the whistles are not the only factor responsible for the enhanced male reaction. The low frequency element seems therefore to be the main factor responsible for this enhanced reaction because of both its presence and its nature. Another argument in favor of this hypothesis is the significant difference found in approaching reactions: no propagation property can be proposed as a relevant explanation to the smaller distance observed in the case of FSS broadcasting once the bird is in the zone. A higher motivated reaction to a specific structure or element seems to be the most natural hypothesis, as it has already been shown in other species (e.g., Water Pipits *Anthus spinol-etta*; Rehsteiner et al. 1998).

Here, we have shown that male Yellowhammers react more strongly to the most complete structure than to the single stereotyped and repeated structure. It had been

suggested in the literature (Catchpole 1980, 1981) that the complete structure was designated to attract females rather than to function in intrasexual selection. We think our result is compatible with this idea. It is indeed possible that the same song structure can be directed to two different receivers and can be interpreted in two different manners.

Females would assess the richness of the song as a good indicator of male value, and assess a potential genitor, which has already been suggested in another playback experiment on Great Tits (*Parus major*) (Otter et al. 1999), when, at the same time, males could assess the value of a potential rival. Although our study was aimed mainly at male behavior, we observed in some cases that the female came along with the tested male she was paired with. We did not find any ornithological data suggesting that female Yellowhammers contribute to the defence of the territory with the male, but we know that female Yellowhammers assess their mate by flying above the already defined territories and choosing the one to which they are the most attracted (Spitz 1995). Therefore, we cannot say if the females were attracted to the playback itself or if they came to help the male defend the territory.

We think that both the low frequency element and the high frequency element play an active part in sexual selection. Although we found that males react more strongly to the FSS structure, maybe because they interpret it as a more aggressive signal, we think that the presence of the terminal phrase is itself an answer to the intersexual selection problem. The presence of this terminal phrase indeed multiplies by four the number of song types that a male can produce. This is of central importance in a species whose repertoire is small (Hansen 1984; Hiatt and Catchpole 1982), especially since it has been shown that females prefer bigger repertoires in this species (Baker et al. 1987). Therefore, the presence of the terminal phrase in Yellowhammers could have been developed as a means to enrich a repertoire in a species where juveniles mainly learn their repertoire from their parents and those in the neighborhood of their natal area, and not from the neighborhood of the breeding area (Hiatt and Catchpole 1982); therefore, we cannot expect an imitation process to enrich this repertoire. The presence of the terminal phrase could have thus been developed as a means to “cheat” on the size of the repertoire, which would not be surprising in passerines, where resident males of a given area are thought to sing different songs to discourage newcomers by giving the impression of a crowded area (see the Beau Geste effect; Krebs et al. 1978; Krebs 1977).

Finally, we found that the low frequency element was more conserved in the population than any other song constituents. The standard deviation around its mean range was indeed nearly half the standard deviation around the mean range of the high frequency element and three times

less than the standard deviation around the mean ranges of the notes. We find it unlikely that a physiological constraint could be the main reason for this smaller variation, given that some of the low frequency notes were found in the same range of variation and with even lower extreme frequencies (unpublished data). Therefore, we think that the low frequency element is an important part of the male song in the Yellowhammer and that this element is more constrained to be produced within a certain range.

Zusammenfassung

Territoriale Reaktionen männlicher Goldammern (*Emberiza citrinella*) auf eine spezifische Gesangsstruktur

Männliche Singvögel schätzen ihre Rivalen ein, indem sie deren Gesang zuhören, und bei einigen Arten reagieren sie besonders empfindlich auf bestimmte Teile des Gesangs. Goldammern (*Emberiza citrinella*) produzieren Gesänge mit unterschiedlichen Strukturen, die aus einer anfänglichen Phrase stereotyper und wiederholter Noten in einem Triller und einer abschließenden Phrase (mal vorhanden, mal nicht) bestehen, die aus niedrig- oder hochfrequenten Pfiffen zusammengesetzt ist, die wir Elemente genannt haben. Wir haben 1,055 Gesänge von 25 unterschiedlichen Männchen aus einer französischen Goldammern-Population untersucht und herausgefunden, dass vier verschiedene Strukturen unterschieden werden konnten. Wir haben beobachtet, dass sich die Frequenzbereiche der Elemente verschiedener Individuen stärker ähnelten als die Notenbereiche und das niederfrequente Element nahezu doppelt so konserviert war wie das hochfrequente Element. Wir haben dann im Freiland die territorialen Reaktionen von Männchen auf die vier verschiedenen Strukturen getestet und herausgefunden, dass die Gesamt-Gesangsstruktur (FSS), die aus der Anfangsphase gefolgt von einem hoch- und einem niederfrequenten Element besteht, stärkere Territoriumsverteidigungsreaktionen der Männchen hervorrief als irgendeine der anderen Strukturen. Da die Struktur, welche nur die Anfangsphase und das niederfrequente Element umfasst, ebenfalls eine starke Antwort auslöste, schlagen wir vor, dass das Hauptelement, das für die stärkere Reaktion der Männchen verantwortlich ist, das niederfrequente Element ist, was mit der Tatsache in Einklang steht, dass es stärker konserviert ist als die anderen Komponenten.

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