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Context-dependent organization of birdsong: experimental evidence from the collared flycatcher, *Ficedula albicollis*

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While acoustic signals are highly flexible, their context-dependent changes remain poorly understood. Birdsong is a model of choice to explore these aspects. As repetition and diversity of song elements largely determine the overall characteristics of signals and such song characteristics as versatility and repertoire size can plastically change in different social contexts, we hypothesized that the repetition of syllables and syllable sequences could also be context dependent. Here, we used the song of the collared flycatcher as a study system. We recorded the song of focal males under different simulated sociosexual contexts (solo singing, intruder male, approaching female and counter-singing situations in the natural environment), and quantified the context-dependent changes in song structure. As well as the commonly used acoustic variables repertoire size, number of syllables in the song and versatility, we also measured the richness (number of different types) and abundance (number of occurrences) of the repeated syllables and syllable sequences in the song bout recorded in different social contexts. We found lower richness of short repeated sequences and a smaller repertoire size in the context of an approaching female compared to the solo context. Conversely, we found higher richness of long repeated sequences and songs with more syllables in counter-singing compared to the solo context in the song of the focal male. Our study provides evidence that the syllable sequences in the song bout can change depending on the social context in collared flycatchers. Our study also emphasizes the importance of considering the repetition-describing characteristics in addition to the commonly used acoustic characteristics when studying animal acoustic communication.

Animal signals can be flexibly changed according to the social context, which facilitates interactions with conspecifics and heterospecifics, thus playing a crucial role in survival and reproduction (Taborsky & Oliveira, 2012). Acoustic signals have been shown to be flexibly expressed in diverse contexts of alarm calling and mobbing (Collier et al., 2020; Templeton et al., 2005), social bonding (Coye et al., 2018; King & Janik, 2013; Lefebvre et al., 2020), food defence (Faragó et al., 2010; Marler et al., 1986), territoriality and courtship (Ammer & Capp, 1999; Araya-Salas et al., 2017; Bohn et al., 2013; Chabout et al., 2015; Rand & Ryan, 1981; Sossinka & Böhner, 1980) in many taxa. On the one hand, receivers of these signals can obtain information about the signaller's quality, identity, inner state and motivation, which help them to make decisions in various situations. On the other hand, the signalling individual may change the acoustic signal according to the presence of the rivals (Geberzahn & Aubin, 2014; Gersick & White, 2018; Logue, 2021; A. S. Opaev, 2022), the sex of the listener (Kipper et al., 2015; Kroodsma et al., 1989; Ronald et al.,

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2015) or other individual quality of the listeners that is important in mate choice (Heinig et al., 2014; Henderson et al., 2018; Jablonszky et al., 2021; Vignal et al., 2004). In this way, the signaller can adjust the signalling cost to the potential threat or gain. Also, it is suggested that different selection processes drive sex-dependent decoding of the signals and, therefore, listener-specific signalling must be adaptive (Cardoso et al., 2007; Leitão et al., 2006; Leitão & Riebel, 2003).

In general, acoustic signals can convey information in diverse ways in the frequency, time and amplitude domains (Aubin & Mathevon, 2020). Furthermore, one of the most fascinating sources of signal diversity is the complexity of acoustic sequences thanks to the potentially large number of combinations of the discrete elements constituting the sequences (Kershenbaum et al., 2016). However, we know particularly little about the context dependence of the sequential structure of acoustic signals (Fishbein et al., 2020). Birdsong is under sexual selection and is the most studied system of sequential signals (Marler & Slabbekoorn, 2004). It is therefore ideal for exploring the organization of acoustic signals as a function of social context. Birdsong consists of short elements, often called syllables, the order of which determines the sequential structure (Brenowitz et al., 1997; Williams, 2004). The repeated syllable types and sequences are often called phrases or motifs (Brenowitz et al., 1997; Janney et al., 2016) and their occurrence can largely shape the compositional characteristics of birdsong in different species (Briefer et al., 2010; Franco & Slabbekoorn, 2009; Markowitz et al., 2013; Riebel, 2009). Beyond the differences between species, the temporal patterns of repeated sequences in song bouts can vary between individual zebra finches, *Taeniopygia guttata* (Bruno & Tchernichovski, 2019). These patterns also appear to be linked to repertoire complexity in pied butcherbirds, *Cracticus nigrogularis* (Janney et al., 2016) and exhibit specific sequential rules at the individual level in canaries, *Serinus canaria* (Markowitz et al., 2013). The question our study focuses on is how the structure of birdsong depends on the social context.

The context-dependent structure of complex birdsong has been studied in a few species, often quantified by syllable or song type switching rates and the number of switching types (A. S. Opaev, 2022). For instance, male house finches, *Haemorhous mexicanus*, exhibit more switching of song types during counter-singing than solo singing and produce longer songs in courtship contexts (Ciaburri & Williams, 2019). Zebra finches adjust motif abundance, while Bengalese finches, *Lonchura striata*, change syllable sequencing depending on the social context (Cooper & Goller, 2006; James et al., 2018; James & Sakata, 2015; Kao & Brainard, 2006; Sossinka & Böhner, 1980). In common chaffinches, *Fringilla coelebs*, the song type switching rate serves as an agonistic signal, matching that of a rival (Deoniziak & Osiejuk, 2020), and songs with more motif types elicit stronger responses (Leitão et al., 2006). These examples highlight species-specific adaptations and the need for broader research to understand the evolutionary mechanisms shaping context-dependent singing.

The song of our model species, the collared flycatcher, has been intensively studied (Garamszegi et al., 2004, 2006, 2007, 2008; Zsebők et al., 2017). In this species, the most often studied basic unit of the song is the syllable which is a short (typically 0.1–0.3 s) vocalization. The syllables are separated by short (typically 0.1–0.2 s) pauses from each other. The songs usually contain about 10 syllables in various sequences without constituting song types which means that typically the content of the songs is not repeated in the same way in the song bout. However, in the song bout, it is possible to find repeated syllable sequences with up to 10 syllables (Zsebők et al., 2021a; see Fig. A1 for example repetitions in the songs). Statistical network analysis has revealed that the sequential organization is age related: older males produce more types of long repeated sequences than younger males (Zsebők et al., 2021a). Listener-dependent acoustic features have also been studied: some song characteristics (including the number of syllable types within a song, the song length, the maximum frequency and the song rate) are adjusted to the individual identity of the receiver (Jablonszky et al., 2021). Furthermore, social context-dependent temporal changes have been found in the song length and maximum frequency of the song (Jablonszky et al., 2022). However, the commonly used characteristics of the song and especially repetitions of the syllables and syllable sequences in such social contexts as solo singing, counter-singing, presence of a female and male intrusion have not been compared in this species.

We hypothesized that collared flycatcher males would change the structure of their songs in different social contexts, as the optimal information encoded in the song may vary with the social situation. We predicted that after male intrusion and in counter-singing contexts males would advertise their experience which can correlate with the age of the bird, the number of learnt syllable types and the number of syllable sequence types as previously shown in this species (Garamszegi et al., 2007; Zsebők et al., 2021a). We also predicted that after the visit of a prospecting female on the territory, the male might advertise its individual and population-specific identity as described in other species (Dunning et al., 2014; Trösch et al., 2017; Wang et al., 2022). To characterize the context-dependent changes in the structure of the song, we included the richness (defined as the number of different types) and the abundance (defined as the number of occurrences) of repeated syllables and sequences. These measures can inform us about the repeating elements in the organization of birdsong, a characteristic that the commonly used measures mentioned above do not provide. With the application of these complex measures, in addition to the commonly used measures like repertoire size, number of syllables in the song and versatility (within-song complexity), we intended to test the predictions given above. Accordingly, we predicted a larger repertoire size and higher richness with fewer repeated syllables and syllable sequences in intrasexual contexts compared to solo singing. Conversely, we predicted a smaller repertoire size, lower richness and more repeated syllables and syllable sequences in intersexual contexts compared to solo singing.

To test our predictions, during the courtship season, we conducted two experiments covering diverse social contexts in a natural population of collared flycatchers. (1) We placed either conspecific male or female stimulus birds on the territory of unpaired singing males to simulate intra- and intersexual contexts to compare with the solo singing context within the territory. We also registered the naturally occurring neighbours songs to control for the counter-singing context. (2) Additionally, we conducted a playback experiment in which we simulated either a singing conspecific neighbour or an individual from another species as a control to study experimentally the effect of the counter-singing context. We then recorded the songs of the focal males and analysed the differences in the repetitions (abundance and richness of syllables and syllable sequences) by the social contexts. We supplemented our analyses with commonly used composition-related acoustic variables (number of syllables in the song, within-song versatility and repertoire size) that were previously found to be context dependent (Balsby & Dabelsteen, 2001; Jablonszky et al., 2022; Nelson & Poesel, 2011; Palmero et al., 2014; Zsebők et al., 2017).

METHODS

Study Species and General Procedures

The collared flycatcher is a small, migratory songbird showing sexual dimorphism (Cramp & Brooks, 1992). After spring migration from Africa, in April, males establish a territory around a nest hole, defend their nesting site against intruding conspecific males and try to attract females by singing close to the nesting site (Eriksson & Wallin, 1986).

We conducted both experiments in the Pilis-Visegrádi Mountains (Hungary), in April and May, between 0600 and 1200 hours, the most active singing period of the day. We made all the song recordings from around 15–20 m away from the nest hole of the focal male. We used a parabolic microphone set (Telinga dish, Sennheiser ME-62 with P6 preamplifier) and digital recorders (Tascam DR1, Microtrack II, Zoom H4n). We recorded at least 20 songs from the focal male. Although it is possible that the focal male detected the experimenter, as the experimental procedure was the same in different contexts, it is unlikely that the presence of the human observer biased our conclusions qualitatively. For the detailed song recording and handling protocol, see Garamszegi et al. (2007; 2006; 2004; 2012).

Experiment with Stimulus Birds

The experiment was conducted in the in the study area (47°43′N, 19°01′E) consisting of around 500 artificial nestboxes during the courtship season of 1999–2016. Most of the nestboxes were installed before 1990, and served as a breeding place for around 100 pairs of collared flycatchers yearly (Herényi et al., 2014).

The protocol of the experiment was as follows. (1) We caught male and female collared flycatchers and (2) presented either of them as a social stimulus to unpaired singing males in their territory; then (3) we recorded the song of the focal singing male. As a control, we also recorded songs from males where no stimulus birds were presented (solo singing situation). After recording the songs, (4) we captured the focal individual. The details of these procedures are given below.

We caught 12 male and 14 female collared flycatchers that were subsequently used as stimulus birds in the experiment. The distance between the site of the experiment and the place of capture of the stimulus birds was greater than 500 m; therefore, it is reasonable to assume that the focal male and the stimulus birds were unfamiliar before the experiment. The stimulus birds were housed in individual cages (40 x 24 cm and 40 cm high) with ad libitum water and food (mealworms) for 3–5 days at the research station house in the field. During the experiment, they were kept in small cages (15x20 cm and 15 cm high) with additional food and they were usually used for no more than one trial per hour. Altogether, each stimulus bird was used in 3.3 ± 2.6 (mean ± SD, range 1–11) trials. Before the release of the birds at the site of capture, we verified that they were in good condition.

Usually, the males sing close to a nestbox to attract the females and actively chase away conspecific males. Based on this conspicuous courtship behaviour, we chose the focal males and their territory for the experiment. First, we presented the focal male with either a male ($N = 43$ cases) or a female stimulus bird ($N = 44$ cases) or an empty cage as a control ($N = 22$ cases). Each focal male was included only once in the experiment with one of the stimuli (between-individual design). Female stimulus birds were placed on the top of the nestbox, mimicking the natural situation when a female inspects a nestbox, while male stimulus birds were positioned at 1–2 m from the nestbox (mimicking a territorial intrusion) for around 5 min. In these experimental situations, the focal male stopped singing and usually invited the female stimulus bird to the hole of the nestbox or aggressively approached the male stimulus bird (Canal et al., 2022; Garamszegi et al., 2014; Szász et al., 2019). The stimulus males did not sing in these situations. Based on these behaviours, we made sure that the focal male detected the stimulus bird, and, hence, we successfully simulated an interested female or an intruder male on the territory. We also noted whether a neighbouring conspecific male was singing during the trial (naturally occurring neighbour song), indicating a natural counter-singing context so that we could control for that in the statistical analysis.

The focal male usually recovered from our interference and began singing again shortly after we removed the stimulus bird from the territory. Thus, we recorded at least 25–30 good-quality songs in the experiment.

Right after the song recording, we caught the focal male with a spring trap set up in the nestbox it guarded. Then, if unringed, we ringed the males with a numbered ring. The age of the males was determined based on plumage characteristics (Svensson, 1984) and our long-term ringing database. Before releasing the males, we marked them with unique colouring using common felt pen on their belly so that we could recognize them without recapturing them during the season and to avoid pseudoreplication. For the detailed handling protocol, see Garamszegi et al. (2007; 2006; 2004; 2012). Altogether, we used the data of 109 individuals in this experiment (Table 1). Some of the data of the recorded individuals were used in other studies with different research questions, and accordingly with different acoustic and statistical analysis (Jablonszky et al., 2021, 2022).

Playback Experiment

The playback experiment was conducted close to the area of the experiment with the stimulus birds, in the Apátkúti valley (47°43′N, 18°59′E) and Bükkös river valley (47°42′N, 18°58′E) without artificial nestboxes during the breeding season in 2017. First, (1) we prepared the playback songs in the laboratory, and then (2) we

Table 1
Sample sizes by year and stimuli in the experiment with stimulus birds

Year	No. of male stimuli	No. of female stimuli	No. of controls	No. of singing neighbours	No. of all experiments
2009	0	24	0	12	24
2010	0	4	0	3	4
2011	0	6	0	4	6
2012	0	0	2	0	2
2013	1	6	6	0	13
2014	4	1	7	0	12
2015	15	1	2	1	18
2016	24	1	5	9	30
Total	44	43	22	29	109

played back conspecific and control songs (other species) from the neighbouring territory to simulate a singing neighbour context. During the playback, we recorded the song of the focal individual. We did not use stimulus birds or catch the focal individual in this experiment.

The playback songs were obtained from the song recordings made in 2016 in the same area, in the same way as described above in a context without any stimulus. This way, we ensured that we played back songs that originated from the same population. We prepared altogether nine playback files from recordings of nine different collared flycatcher males, each file containing songs exclusively from a single flycatcher. Each playback sequence contained a period of 15 songs (3−5 s long songs with 5−10 syllables in each and a 3−5 s pause between them) lasting 2 min plus 2 min silence, resulting in a 4 min long playback file that was played back repeatedly in the experiment. We also prepared one song sequence containing 15 songs from three European robins, *Erithacus rubecula*, as a control stimulus in the same way. The background noise of the recordings was eliminated with the Lasso tool in Adobe Audition 3.0 (Adobe System Inc., San Jose, CA, U.S.A.).

After finding a frequently singing male collared flycatcher, we observed its behaviour for at least 10 min. We ensured that no female visited the nest hole and estimated the borders of its territory by tracking its movements. Usually, these males were guarding an area with a radius of about 15 m around their natural nest hole. We placed the playback equipment (Sony SRS-XB3G Portable Wireless Speaker) outside the estimated territory, around 20 m from the nest hole. For the song recording, we chose a position where both the speaker and the nest hole were about 20 m from us. The playback was controlled from a mobile phone via a wireless Bluetooth connection. We played back a random conspecific sequence file and the control sequence file, each for 16 min in a random order. The sound amplitude was kept standard across the trials (85 dBA from 1 m from the speaker) and chosen to be similar to the natural loudness of the collared flycatcher. This loudness was found to be effective in eliciting responses in an earlier playback study (Vaskuti et al., 2022). Usually, the focal bird reacted to a conspecific male immediately (but not to the control playback), explored the close vicinity of the speaker and spent considerable time between the speaker and the nest hole while singing. During the playback, we simultaneously recorded the song of the focal male in the same way as described above. If any doubt arose about the circumstances and the pairing status of the male, we discontinued the trial and did not include it in our analysis. Altogether, we managed to conduct trials successfully with 16 males.

Acoustic Processing

The acoustic analyses were performed with the Ficedula Toolbox (open-source, freeware, https://github.com/zsebok/Ficedula, Zsebők et al., 2018). We used only good-quality recordings without much background noise. We cut out the songs from the recordings and segmented the syllables by marking the start and endpoints, as well as the minimum and maximum frequencies, of each syllable on the spectrographic view of the songs. Note that the time and frequency information of the segmented syllables was only used by the Ficedula Toolbox to calculate the similarity between the syllables (Zsebők et al., 2018). We manually categorized the segmented syllables into syllable types based on their spectrographic similarity, in which process the Ficedula Toobox showed the similar syllables next to each other. Previously, the computer-aided manual clustering process with the Ficedula Toolbox had proved to be highly repeatable between observers (Cohen's $\kappa = 0.87$, Zsebők et al., 2018). We used the data for the first 20 consecutive songs from each recording in all statistical analyses. Based on the output of the program, we calculated the following acoustic variables: the average number of syllables in the songs, the average within-song versatility (number of syllable types in the song divided by the number of syllables in the song), and the repertoire size (number of different syllable types in 20 songs) for each recording. When we processed the recordings from the playback experiment, we paid special attention to identifying the songs of the focal male, distinguishing them from the playback by visually examining the spectrogram.

We defined a repeated syllable or repeated syllable sequence as one that appeared in at least two songs in the 20 songs sampled. We used a custom-made script in the R environment (R Core Team, 2018) to find the repeated syllables and syllable sequences with a length of two to eight syllables. For that, the script scanned through all the 20 songs for the syllables and syllable sequences and identified those that occurred in more than one song. Then, the script counted the songs in which the particular syllable or syllable sequence occurred. We determined the maximum length of the repeated syllable sequence, measured by the number of syllables, based on the findings of Zsebők et al. (2021b), which revealed that 50% of the recordings contained repeated syllable sequences with eight syllables, and longer repeated sequences were even rarer. After finding all the repeated syllables and syllable sequences in the 20 songs, we calculated the richness (R) defined by the number of different repeated syllables and syllable sequences for each length which we refer as R1, 2, …, 8 (where the number after R refers to the length of the sequence; see Fig. 1 for examples). For each repeated syllable and syllable sequence, we also obtained the number of songs in which that syllable or syllable sequence occurred. These occurrences were averaged for the syllables and each syllable sequence length; we refer to them as abundance A1, 2, …, 8 (see Fig. 1 for examples). Note that in this way, we did not account for multiple occurrences of syllable or syllable sequences within the songs. For the descriptive statistics of the variables, see Table A1.

We calculated the pairwise Pearson correlations between all the measured variables based on the data of the 109 recorded individuals. We found that measured variables (repertoire size, versatility, number of syllables in the song, R1 - 8, and A1 - 8) were not independent of each other (Table A2). Specifically, we found stronger correlations among the R1 - 8 variables when the lengths of the sequences were more similar. A similar pattern was observed for the A1 - 8 variables. This phenomenon can be attributed to the fact that longer repeated sequences inherently encompass shorter repeated sequences. However, note that shorter sequences can be combined in various ways, resulting in different longer sequences (Fig. A1). To decrease the number of variables in the statistical analysis, we kept richness and abundance variables related to sequences with two and eight syllables (R2, R8 and A2, A8) to characterize the repetitions in both short and long sequences. We also kept the repertoire size, versatility and syllable number in the song to characterize the commonly studied aspects of birdsong. In this way, we kept both diversity- and repetition-related variables in the analyses and conducted the analyses for fewer characteristics.

Statistical Analysis

Regarding the experiment with the stimulus birds ($N = 109$), we investigated the effect of social contexts on the different acoustic variables separately with generalized linear mixed models (GLMMs) with the 'lme4' library in R (Bates et al., 2015). For each acoustic variable (i.e. number of syllables, repertoire size, versatility, R2, R8, A2, A8), we built a model where the given acoustic variable was the dependent variable (in total seven models). We included the context-describing variables as follows: stimulus type as a three-level factor (male stimulus, female stimulus and control

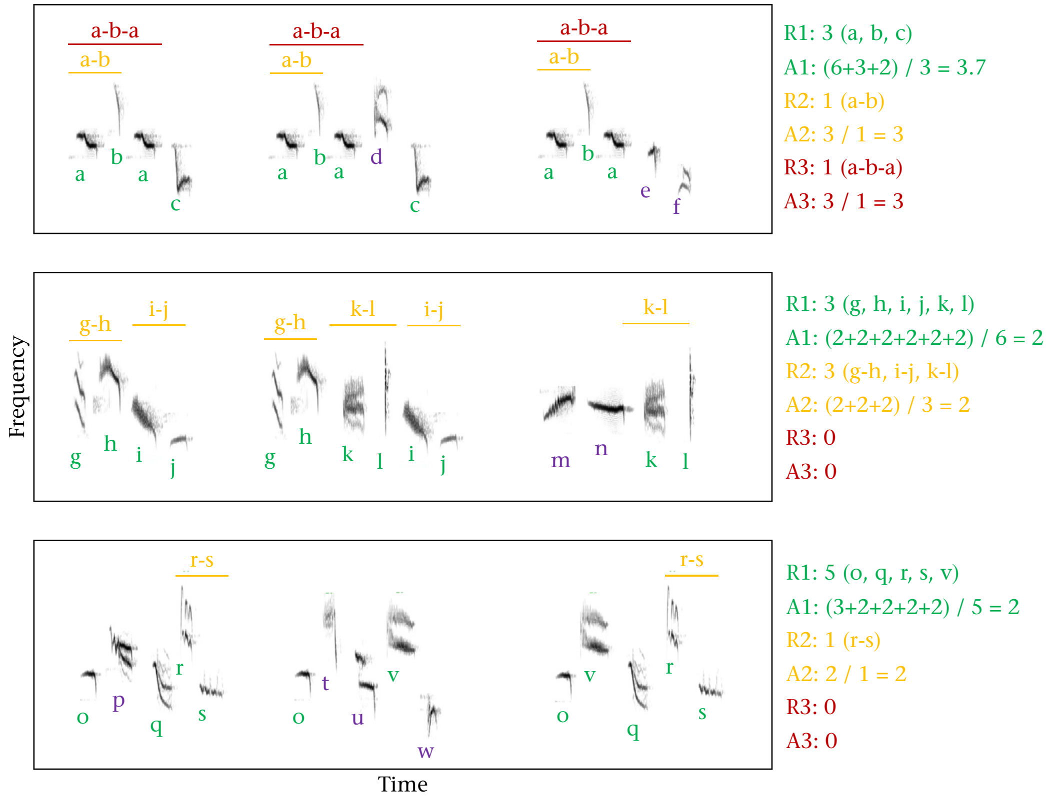

Figure 1. Richness and abundance of repeated syllables and syllable sequences in the song of the collared flycatcher. Each spectrogram shows three songs. Syllable types are indicated under the syllables with unique letters. Repeated syllables and syllable sequences are indicated with different colours depending on the length (repeated syllable: green; two-syllable-long sequence: yellow; three-syllable-long sequence: red). Unrepeated syllables are in purple. The richness (R1 - R3) and abundance (A1 - A3) of the repetitions are shown to the right of the spectrogram. We defined richness as the number of different repeated syllable types or repeated syllable sequence types, and abundance as the average number of occurrences of the repeated syllable types or repeated syllable sequence types. Additionally, we obtained the repertoire size (number of syllable types in all songs), the average number of syllables in the songs and the versatility (average of the number of syllable types divided by the number of syllables in each song). For simplicity, we calculated the values for these sequences based on the three songs represented in each spectrogram. However, the calculations were made on 20 songs in the study (see Methods).

situation when no stimulus was presented) and the presence of a naturally singing neighbour during song recording as a binary factor. We included the age of males as a binary variable (juvenile: 1 year old; adult: more than 1 year old) in the model, as previous findings indicated that the song characteristics change with the age of the singing male (Garamszegi et al., 2007; Zsebők et al., 2021a, 2021b). As the intensity of the courtship behaviour changes within the season, we also included the arrival date as the date of the experiment relative to the median of the arrivals of the males in the given year (Canal et al., 2022). Additionally, we included the year and the ID of stimulus birds as random factors. We included the interaction of stimulus type and the neighbour's song as we predicted different reactions to the stimuli when a singing neighbour was present. We checked the distribution of the residuals with the help of 'DHARMa' library (Hartig, 2021). We applied negative binomial generalized linear models when Gaussian models produced unsatisfactory residual distributions.

As several experimental and environmental variables were incorporated into the models, we initially conducted a model selection procedure using the dredge function from the 'MuMIn' library (Bartoń, 2023). The optimal model was selected based on the corrected Akaike information criterion (AICc) value. For repertoire size, all terms were included in the model. For versatility, the best model was the null model, which contained no fixed terms. Details of the model selection results are provided in the Supplementary Material. To characterize the effect of the different social contexts, we obtained the estimation of the fixed effects with their bootstrap confidence interval based on 1000 simulations. We also calculated the partial effect sizes (η^2) with the 'sjstats' library (Lüdecke, 2022).

Regarding the playback experiment ($N = 16$ males), we also built a GLMM with each acoustic variable (seven models in total). We included the type of stimulus as a binary fixed effect (playback of flycatcher or control songs), and the order of the given stimulus also as a binary fixed effect (first or second playback in the experiment), and the ID of the focal individual as a random factor. We used negative binomial generalized linear models when Gaussian models produced unsatisfactory residual distributions. To characterize the effect of the playback, we obtained the estimation of the fixed effects with their bootstrap confidence interval based on 1000 simulations, and calculated the partial η^2 effect sizes.

To interpret the statistical results, we considered those effects significant where the confidence intervals of the estimations did not include 0. In these cases, we interpreted the partial η^2 effect sizes as small ($0.01 \leq \eta^2 < 0.06$), medium ($0.06 \leq \eta^2 < 0.14$) and large ($\eta^2 \geq 0.14$) according to Cohen (1988).

Ethical Note

Permissions for the fieldwork were obtained from the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management, ref. no's: KTVF 16360-2/2007, KTVF 30871-1/2008, KTVF 43355-1/2008, KTVF 45116-2/2011, KTVF 21664-3/2011, KTVF 12677-4/2012, KTVF 10949-8/2013, PE/EA/101-8/2018, PE-06/KTF/8550-4/2018, PE-06/KTF/8550-5/

2018) and the work was approved by the ethical committee of the Eötvös Loránd University (ref. no. TTK/2203/3). All applicable international, national and/or institutional guidelines for the care and use of animals were followed. Housing conditions for the stimulus birds, as well as their handling and the experimental procedures, were designed to minimize welfare impacts. The birds were provided with ad libitum food and water and were disturbed only during the experimental procedures by expert biologists. The stimulus birds were not injured in the experiments and were frequently found successfully breeding in the population.

RESULTS

Experiment with Stimulus Birds

We found several significant effects of social contexts on different acoustic variables, where the confidence intervals of the fixed effects did not include zero. In these cases, the effect sizes we obtained ranged from 0.06 to 0.09, which are considered medium effect sizes (Table 2, Fig. 2).

Concerning the richness of repeated syllable sequences in the songs of the focal male, the presence of naturally singing neighbours was related to more types of long syllable sequences repeated than in the solo singing context indicated by the positive medium effect for variable R8. In the context of the female stimulus, we found a medium negative effect for variable R2 indicating a song production with fewer types of short syllable sequences repeated in this context compared to the solo singing context. We found little effect of any social context on the abundance of sequences but a medium positive effect of the presence of naturally singing neighbours on the number of syllables. Female stimulus had a medium negative effect on the repertoire size. In the male stimulus context, we found little evidence of any social context effect on the song variables.

We also found that the age of the focal males had a large positive effect on the repertoire size, a medium positive effect on the richness of the long repeated sequences (R8) and a medium negative effect on the abundance of short syllable sequences (A2; Fig. A2). The date of arrival had a medium positive effect on the repertoire size (Fig. A3).

Playback Experiment

We found a large positive effect ($\eta^2 = 0.32$) of the flycatcher song playback on the abundance of short repeated sequences (A2; Table 3, Fig. 3). Additionally, we found that the order of the playback (control/flycatcher) sequence also had a large positive effect ($\eta^2 = 0.33$) on A2, which means that the flycatcher song playback in the first round had a carryover effect on the control playback in the second round. We found no other acoustic variables that would be significantly affected by the playback.

DISCUSSION

By recording male songs under different simulated social contexts (solo singing, intruder male, prospecting female and counter-

Table 2
Statistical results of the effect of social contexts on birdsong obtained from GLMMs

		Intercept	Singing neighbour	Female stimulus	Male stimulus	Age	Arrival	Neighbour: female stimulus	Neighbour: male stimulus	V_{year}	$V_{stimulus\ ID}$	$V_{residuals}$
Repertoire size	β ± SD	40 ± 4.1	19.7 ± 18.1	-10.7 ± 5.2	-1.5 ± 4.8	24 ± 3.6	1.5 ± 0.4	-25.8 ± 18.8	-21.9 ± 19.4	0.0	0.0	301.0
	CI	31.2–48.2	-15.8–56.6	**-21–-0.9**	-11–8.5	**16.5–31**	**0.8–2.2**	-64.8–11	-63.1–15.8	0–0	0–0	229.4–407.3
	z	9.7	1.1	**-2.1**	-0.3	**6.7**	**3.9**	-1.4	-1.1			
	P	0.000	0.279	**0.041**	0.756	**0.000**	**0.000**	0.175	0.261			
	η^2		0.00	**0.06**		**0.26**	**0.09**	0.01				
No. of syllables	β ± SD	9.8 ± 0.6	**5.2 ± 2.4**	-1.4 ± 0.7	-0.1 ± 0.7	0.9 ± 0.5		-3.8 ± 2.5	-4.8 ± 2.5	0.4	0.0	5.2
	CI	8.6–11	**0.8–9.8**	-2.7–0.1	-1.4–1.3	-0.1–1.9		-8.7–0.7	-9.8–0.1	0.1–0.8	0–0	3.9–6.8
	z	16.1	**2.2**	-1.9	-0.1	1.9		-1.6	-1.9			
	P	0.000	**0.031**	0.068	0.908	0.057		0.124	0.057			
	η^2		**0.06**	0.06		0.03		0.03				
Versatility	β ± SD	0.7 ± 0.0								0.0	0.0	0.0
	CI	0.7–0.7								0.0–0.0	0.0–0.0	0.0–0.0
	z	78.0										
	P	0.000										
	η^2											
R2	β ± SD	30.9 ± 2.9	17.3 ± 11	**-7.8 ± 3.4**	1.2 ± 3.1	3.4 ± 2.3		-15.1 ± 11.5	-15.2 ± 11.7	9.2	0.0	112.6
	CI	25.2–36.8	-6.3–41.2	**-14.9–-1.2**	-5.2–7.4	-0.9–7.7		-39.4–10.1	-40.2–9.2	2.3–20.1	0.0–0.0	84.9–150,2
	z	10.8	1.6	**-2.3**	0.4	1.5		-1.3	-1.3			
	P	0.000	0.119	**0.028**	0.713	0.138		0.193	0.197			
	η^2		0.03	**0.09**		0.02		0.02				
R8	β ± SD	-0.2 ± 0.3	**0.8 ± 0.3**			**0.9 ± 0.3**				0.2	0.0	
	CI	-0.8–0.3	**0.2–1.6**			**0.3–1.5**				0.1–0.5	0.0–0.1	
	z	-0.7	**2.4**			**2.6**						
	P	0.483	**0.015**			**0.010**						
	η^2		**0.08**			**0.06**						
A2	β ± SD	3.1 ± 0.2	0.4 ± 0.2			**-0.7 ± 0.2**				0.1	0.0	0.8
	CI	2.7–3.4	0–0.8			**-1–-0.3**				0–0.2	0–0	0.6–1.1
	z	17.7	2.0			**-3.6**						
	P	0.000	0.053			**0.000**						
	η^2		0.03			**0.11**						
A8	β ± SD	-0.8 ± 0.2	0.4 ± 0.3			0.4 ± 0.3				0.0	0.0	
	CI	-1.3–-0.4	-0.1–0.9			-0.1–1				0–0	0–0	
	z	-3.7	1.7			1.6						
	P	0.000	0.086			0.104						
	η^2		0.05			0.03						

Bold values show results where the confidence intervals of the estimation of fixed effects do not include zero ($N = 109$ individuals). R2 and R8 represent the richness of syllable sequences with two and eight syllables, while A2 and A8 represent the abundance of syllable sequences with two and eight syllables, respectively.

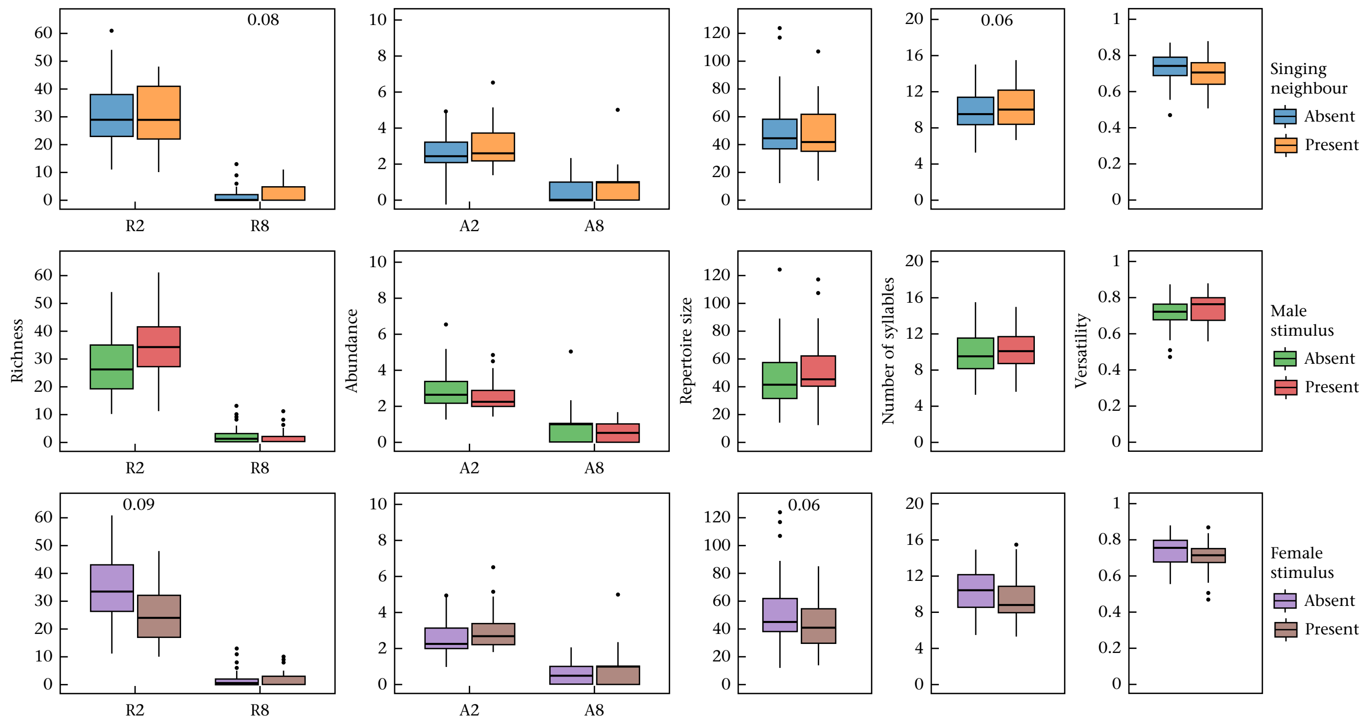

Figure 2. The effect of social context on the song variables. The acoustic variables are shown in the columns and the social contexts are arranged in the rows. The numbers after R and A labels specify the length of the repeated sequence. The colours indicate whether the song was recorded in the given social context. The effect sizes obtained from the GLMM are shown when the confidence intervals of the estimated effects do not contain 0. Note that the graphs show the distribution of original data. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

singing situations) in the natural environment, we found that collared flycatcher males were able to adjust some characteristics of their songs according to some of the social contexts. We found that both the simple descriptive acoustic variables, such as the repertoire size of the syllables and the number of syllables in the song, as well as the variables describing song organization, such as the abundance and richness of the repeated sequences, are affected by the singing neighbour or the presence of a female on the territory compared to the solo singing context.

The two experiments supported the differential use of repetitions in the counter-singing context versus solo singing. In the stimulus bird experiment, we used the information of the occurrence of a naturally singing conspecific neighbour as non-manipulated contextual data; this revealed the relationship between the song features of the focal male and the presence of a singing neighbour in a between-individual comparison (cross-sectional approach) but not whether the latter caused focal males to change their song. It could be that (1) the neighbour's song initiated the change in the song of the focal male or (2) neighbours were more likely to sing when the focal male sang with specific acoustic characteristics. By contrast, in the playback experiment, we actively simulated the singing neighbour context; thus, the within-individual changes can be directly attributed to the song of the conspecific neighbour. In both experiments, in the counter-singing context, the songs of the focal male tended to have more repeated short syllable sequences, although this was only significant in the playback experiment. Focal males also tended to produce songs with a higher richness of the long repeated syllable sequences; however, this phenomenon was significant in the experiment with stimulus birds.

We observed little effect of the counter-singing context on repertoire size and versatility and only a medium positive effect on the number of syllables in the experiment with stimulus birds. Regarding variables associated with repetition, it seems that collared flycatcher males have the capacity to sing songs with more syllables in a way that includes a diversity of repeated long syllable sequences. Theoretically, without changing repertoire size, this could be achieved by recombining the same syllable types in different ways within their songs. However, it is also plausible that males utilize different syllable types in similar numbers to construct syllable sequences with increased richness in long repeated sequences. A more detailed sequential analysis is required to fully explain these changes, but it falls outside the scope of the present study. This phenomenon is similar to the findings in house finches, where the syntax diversity and the number of syllable transitions were higher with an unchanged number of syllable types in the counter-singing context compared with the solo context (Ciaburri & Williams, 2019). The increase in number of syllables in the song can also contribute to the increase in abundance of the short repeated sequences that we observed in both experiments, although this was significant only in the playback experiment. However, note that an increased number of syllables in the song does not necessarily result in an increased abundance of repeated sequences as syllables can combine in various ways. Therefore, our study highlights that the richness and abundance of repeated syllable sequences can give further insights into the context dependency of birdsong as well as the previously found characteristics (Nelson & Poesel, 2011; A. S. Opaev, 2022). The increased richness of the repeated long sequences can be understood as a song bout with more structured songs, that is, with less sequential variance between the songs. This finding can lead us to a testable prediction about the similarity in the evolutionary mechanisms shaping context-dependent singing of species with and without song types by quantifying the repeated syllable sequences in general and in the counter-singing context specifically (A. S. Opaev, 2022).

Table 3
Statistical results of the effect of playback obtained from GLMMs

		Intercept	Playback type	Order of playback	V_{id}	$V_{residuals}$
Repertoire size	β ± SD	66.8 ± 6.6	0.1 ± 3.1	-2.6 ± 3.1	584.9	85.2
	CI	53-4 – 80.5	-6.3–5.8	-21–-0.9	440.6–753.4	50.8–141.1
	z	10.1	0.0	0.8		
	p	0.000	0.984	0.426		
	η^2		0.00	0.04		
No. of syllables	β ± SD	10.2 ± 0.5	0.2 ± 0.3	0.3 ± 0.3	3.6	0.7
	CI	9.0–11.3	-0.3–0.8	-0.3–0.9	2.5–4.8	0.4–1.2
	z	19.0	0.8	1.1		
	p	0.000	0.430	0.275		
	η^2		0.04	0.08		
Versatility	estimate	0.844 ± 0.016	-0.014 ± 0.009	-0.014 ± 0.009	0.0	0.0
	CI	0.81–0.877	-0.032–0.003	-0.033–0.004	0.002–0.005	0.000–0.001
	z	51.4	-1.6	-1.6		
	p	0.000	0.137	0.130		
	η^2		0.14	0.15		
R2	β ± SD	30.9 ± 3.3	0.7 ± 2.2	-0.4 ± 2.2	111.9	40.3
	CI	23.8–37.6	-4.0–5.2	-4.9–4.0	74.3–165.4	25.7–74.4
	z	9.4	0.3	-0.2		
	p	0.000	0.764	0.848		
	η^2		0.01	0.00		
R8	β ± SD	-3.6 ± 1.1	1.2 ± 0.6	0.7 ± 0.6	4.5	
	CI	-5.7–-1.7	-0.1–2.4	-0.6–1.9	2.2–7.4	
	z	-3.2	2.0	1.1		
	p	0.001	0.044	0.252		
	η^2		0.23	0.11		
A2	β ± SD	1.99 ± 0.147	**0.091 ± 0.035**	**0.093 ± 0.035**	0.3	0.0
	CI	1.693–2.297	**0.019–0.16**	**0.024–0.162**	0.292 – 0-373	0.006– 0-018
	z	13.5	**2.6**	**2.6**		
	p	0.000	**0.022**	**0.020**		
	η^2		**0.32**	**0.33**		
A8	β ± SD	-2.2 ± 0.9	0.0 ± 0.7	0.6 ± 0.7	1.1	
	CI	-3.9–-0.6	-1.5–1.5	-1.0–2.4	0.4–1.9	
	z	-2.6	0.0	0.8		
	p	0.010	0.999	0.410		
	η^2		0.00	0.04		

Bold values show results where the confidence intervals of the estimation of fixed effects do not include zero ($N = 16$ individuals). R2 and R8 represent the richness of syllable sequences with two and eight syllables, while A2 and A8 represent the abundance of syllable sequences with two and eight syllables, respectively.

Contrary to our initial prediction, in the counter-singing context, focal males showed no increase in repertoire size of syllables and no decrease in the abundance of repeated syllable sequences. Theoretically, diverse, repeated long syllable sequences can be advantageous in signalling individual identity as repetition can make it easier for conspecific birds to memorize the song of the focal bird, and diverse sequences can be individual specific. Individual-specific songs might be adaptive in neighbour - stranger discrimination by, for example, effectively reducing the cost related to territorial defence (Carlson et al., 2020). While we did not examine the individuality of sequences in this study, Garamszegi et al. (2012) found that individual males in the same population share only around 30% of their syllable types. Therefore, males presumably possess individual-specific repertoires but may also express individual-specific syllable sequences which can facilitate neighbour recognition.

Note that the slight differences in the results between the two experiments suggest that we cannot entirely exclude the possibility that a singing style with a higher richness of long repeated syllable sequences may elicit an aggressive response and a counter-singing behaviour from the neighbours similar to the cases of species with song types where the within- and between-song organization of syllables affects the neighbours' responses (Botero & Vehrencamp, 2007; Kramer et al., 1985; Searcy & Beecher, 2009). An alternative explanation can be that in the counter-singing context collared flycatcher males react differently to familiar neighbours (like naturally singing neighbours in our experiment with bird stimuli) and to unfamiliar neighbours (like the simulated singing neighbour in our playback experiment) similar to other species (Briefer et al., 2008; Moser-Purdy & Mennill, 2016; Skierczyn et al., 2007). Finally, we also cannot rule out that the playback set-up was not as effective as the natural situation of a counter-singing context. Further set-up improvement can be achieved by combining the playback with the presence of a live conspecific male stimulus (Cruz et al., 2022).

The experimental simulation of the departure of a prospecting female led to a decrease in the richness of repeated short syllable sequences and a reduction in repertoire size compared to the solo condition. The decreased repertoire size of the syllables could have contributed to the lower number of different short syllable sequence types. Also, the number of syllables in the song tended to be lower in this situation, and, while this was not significant, it could also partially contribute to the decreased diversity of short syllable sequences. Previously we found no clear relationship between repertoire size and pairing success in our model species (Garamszegi et al., 2004, 2008); therefore, we predicted that males would not increase their repertoire size in a female-visiting social context, but would use special syllable types or sequences to attract the female to the nest hole. While the decreased repertoire size and decreased richness of short sequences were aligned to our prediction, we did not observe an increase in the abundance of the short repeated sequences compared to the solo situation. Without any further experimental evidence, we can only speculate how the changed song characteristics function in female choice. It is possible that females may prefer males with consistent song content (Byers, 2007; Taff & Freeman-Gallant, 2016; Tobin et al., 2019), which may be more likely expressed in songs with a small repertoire size. Similarly, in blue tits both repertoire size and consistent

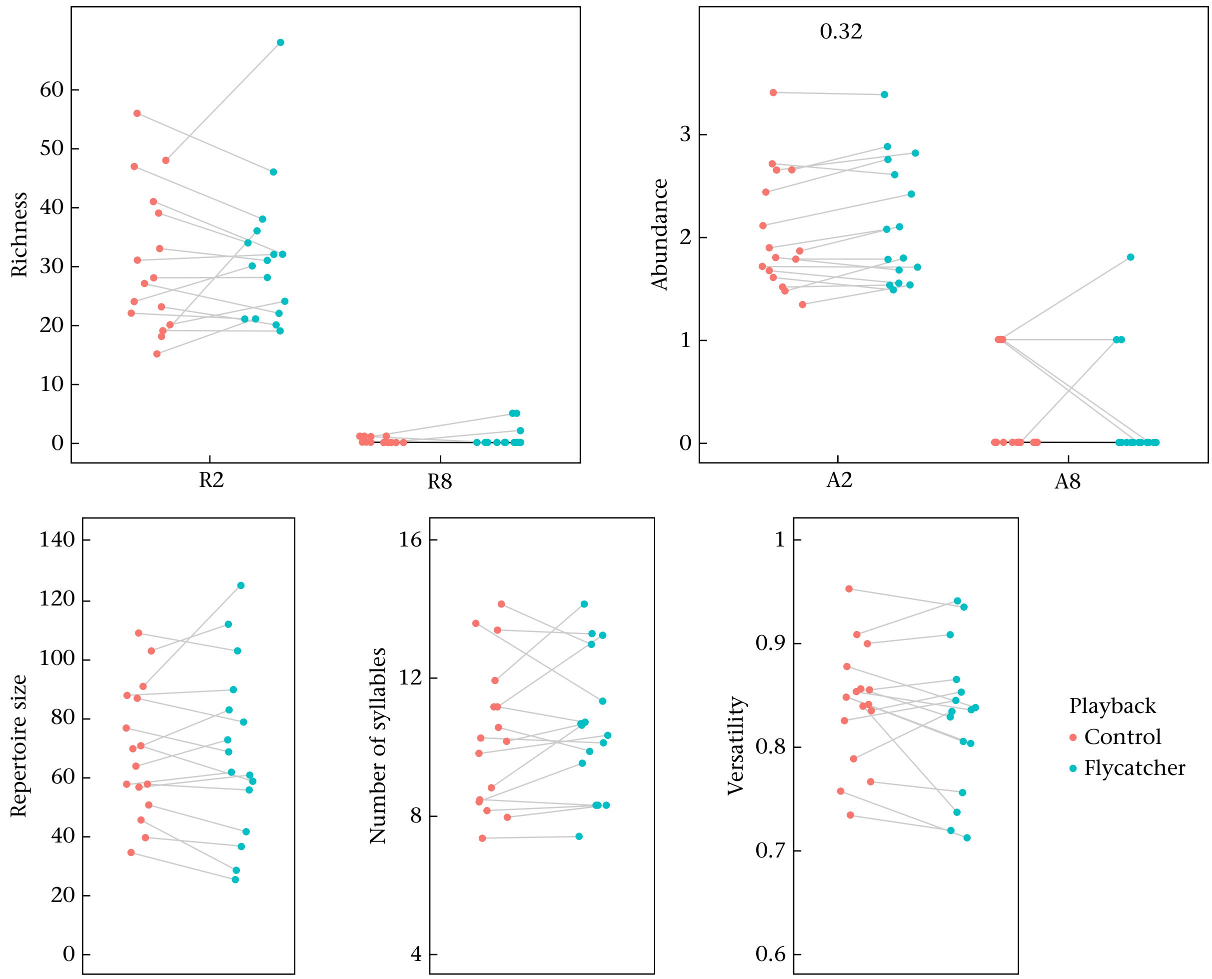

Figure 3. The effect of playback on the song variables. The numbers after R and A labels specify the length of the repeated sequence. Each line indicates a within-individual change ($N = 16$ individuals). For Abundance the effect size obtained from the GLMM is shown as the confidence intervals of the estimated effects do not contain 0. Note that the graphs show the distribution of original data.

repetition shape the song (Sierro et al., 2023). It is also plausible that males sing songs towards females with syllable types commonly occurring in the population to signal their origin. The latter may be adaptive if females prefer males with songs of the local dialect, as described in other species (Slabbekoorn & Smith, 2002). Our experimental situation, involving a female that had recently departed from the territory, is similar to the context used in laboratory settings to induce female-directed song production in zebra finches (Cooper & Goller, 2006; James et al., 2018; Kao & Brainard, 2006). However, contrary to our results, the abundance of motifs in the zebra finch songs increases in this context, suggesting different species-specific optimizations for context-dependent usage of repeated sequences.

We found little effect of male intrusion on song characteristics compared with solo singing. Jablonszky et al. (2021) also studied the song characteristics of collared flycatchers in the male intrusion context; however, they focused on the effect of the identities of the focal and intruder males on the song and not on the between-context differences. Nevertheless, they found considerable variance in several song characteristics between focal males in this context which can blur the effect of male intrusion on the song of the focal male. It is also possible that focal males changed these characteristics of the song after a male visit that we have not measured. For example, we did not extract information about the song rate as we were interested in the syllable organization of the songs. However, there are studies in other bird species that emphasize the role of song rate in territorial defence and as a signal of the level of aggression (De Kort et al., 2009; A. S. Opaev, 2022; Opaev et al., 2019; Szymkowiak & Kuczyński, 2017). Further experimental studies with a within-individual repeated design that focus on other song characteristics may clarify this question.

In addition to the context-dependent changes in song composition, our results also indicate that males' age and arrival date are related to several song characteristics. Compared with juvenile males, older males tended to exhibit a larger syllable repertoire, songs with more syllables, greater richness primarily of the medium and long repeated syllable sequences and a lower abundance of syllable sequences, especially in short sequences. These results align with previous findings in our study species (Garamszegi et al., 2007; Zsebők et al., 2021a). The age-dependent use of repeated syllable sequences resembles the results in Bengalese finches, where song sequences were shown to be more stereotyped in older males (James & Sakata, 2014), as well as in common nightingales, *Luscinia megarhynchos*, where older individuals produced longer song sequences with distinct songs (Weiss et al., 2014). Interestingly, the effects of arrival date were similar to the effects of age: later arriving males had a larger repertoire. The positive relationship between arrival date and repertoire size was opposite to the previous findings in common nightingales (Kipper et al., 2006). Note that according to our protocol, we visited the nestbox sites every day and searched for singing males. Therefore, we used the date of the experiment as a proxy of the arrival of the focal male. However, it is possible that a focal male that we sampled had arrived earlier and sang in his second territory. To disentangle the effect of the date when the bird arrived and the time elapsed from the arrival of the male to the experiment, we need to conduct repeated measurements. Moreover, further within-individual studies are required to investigate the extent to which individual quality and changing social dynamics during the courtship season can elucidate the impact of the arrival date on male song in collared flycatchers.

As the acoustic characteristics of the song and social interactions may vary according to environmental conditions (e.g. Strauß et al., 2020), studies with across-subject and across-year designs can be influenced by these varying conditions. While our study included a large number of individuals with somewhat unbalanced sampling by social contexts in the across-subject examination, we statistically controlled for the effects of year and season. Future studies with a within-subject design could eliminate this limitation of our approach and provide more robust results.

Conclusions

We have shown that collared flycatcher males adjusted the repetition of the syllable sequences in their songs according to the current social context. We found that both the richness and the abundance of repeated syllable sequences can be changed. Acoustic measurements, such as the number of syllables in the song and repertoire size, revealed only partially the context-dependent characteristics of the songs. While these acoustic traits proved influential in female choice and territorial contexts to advertise individual quality, they do not inform about the structure of the syllable sequences. Thus, we emphasize that combining the commonly used simple acoustic measures and the repetition-describing variables (richness and abundance of the repeated sequences) can be a powerful tool for revealing details that may have a crucial function in the acoustic communication of animals.

Author Contributions

David Canal: Writing – review & editing, Investigation. **Éva Vaskuti:** Writing – review & editing, Investigation, Data curation. **Gergely Nagy:** Writing – review & editing, Investigation. **Karola Anna Barta:** Writing – review & editing, Investigation. **László Zsolt Garamszegi:** Writing – review & editing, Supervision, Project administration, Investigation, Conceptualization. **Miklós Laczi:** Writing – review & editing, Investigation. **Mónika Jablonszky:** Writing – review & editing, Investigation, Formal analysis. **Sándor Zsebők:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sébastien Derégnaucourt:** Writing – review & editing.

Data Availability

The data for this study are available in the Supplementary material.

Declaration of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.11.004.

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Appendix

Table A1
Descriptive statistics of the acoustic variables

Acoustic variable	Mean ± SD	Minimum - maximum
Repertoire size	48.3 ± 20.9	12–124
No. of syllables in the song	10 ± 2.4	5.3–15.5
Versatility	0.7 ± 0.1	0.5–0.9
R1	25.7 ± 10	7–60
R2	30.4 ± 11.4	10–61
R3	23.5 ± 9.1	6–52
R4	16.3 ± 7.5	1–39
R5	10.7 ± 6.5	0–32
R6	6.6 ± 5.5	0–29
R7	3.7 ± 4.1	0–19
R8	1.8 ± 2.7	0–13
A1	4.9 ± 1.5	2.5–10.4
A2	3.7 ± 1	2.2–7.5
A3	3.3 ± 1	2.1–6.9
A4	3.1 ± 1	2–7.8
A5	2.7 ± 1.1	0–8.7
A6	2.3 ± 1	0–8
A7	1.7 ± 1.2	0–6.7
A8	1.2 ± 1.2	0–6

The numbers 2–8 after R (richness) and A (abundance) specify the length of the repeated sequence, while 1 refers to repeated syllables.

Table A2
The correlative relatedness of the acoustic variables

	Repertoire size	Syllables in song	Versatility	R1	R2	R3	R4	R5	R6	R7	R8	A1	A2	A3	A4	A5	A6	A7
Syllables in song	0.7																	
Versatility	0.3	0.0																
R1	0.9	0.7	0.3															
R2	0.5	0.8	0.2	0.7														
R3	0.4	0.8	0.1	0.6	0.9													
R4	0.3	0.7	0.0	0.5	0.7	0.9												
R5	0.2	0.6	-0.1	0.3	0.4	0.7	0.9											
R6	0.2	0.5	-0.1	0.2	0.3	0.5	0.8	0.9										
R7	0.1	0.4	-0.1	0.2	0.2	0.4	0.7	0.8	0.9									
R8	0.1	0.4	-0.1	0.2	0.2	0.4	0.6	0.8	0.9	0.9								
A1	-0.7	-0.2	-0.1	-0.7	-0.3	-0.2	-0.1	0.0	0.0	0.1	0.1							
A2	-0.7	-0.3	-0.3	-0.7	-0.5	-0.3	-0.1	0.1	0.2	0.2	0.2	0.8						
A3	-0.6	-0.3	-0.4	-0.6	-0.5	-0.4	-0.1	0.1	0.2	0.3	0.2	0.6	0.9					
A4	-0.5	-0.2	-0.4	-0.5	-0.5	-0.3	-0.1	0.1	0.2	0.3	0.3	0.5	0.8	0.9				
A5	-0.4	-0.1	-0.4	-0.3	-0.3	-0.2	0.0	0.2	0.3	0.4	0.3	0.5	0.7	0.8	0.9			
A6	-0.3	0.0	-0.5	-0.2	-0.2	-0.1	0.1	0.3	0.3	0.4	0.4	0.4	0.6	0.7	0.8	0.9		
A7	-0.1	0.2	-0.4	0.0	-0.1	0.1	0.3	0.4	0.5	0.5	0.5	0.2	0.4	0.4	0.6	0.7	0.8	
A8	0.0	0.2	-0.3	0.0	-0.1	0.1	0.3	0.4	0.5	0.6	0.6	0.2	0.4	0.4	0.5	0.7	0.7	0.8

The matrix contains the Pearson correlation coefficients calculated between all variables pairwise. The numbers 2–8 after R (richness) and A (abundance) specify the length of the repeated sequence, while 1 refers to repeated syllables. The bold variable names indicate that the variable was included in the statistical analyses.

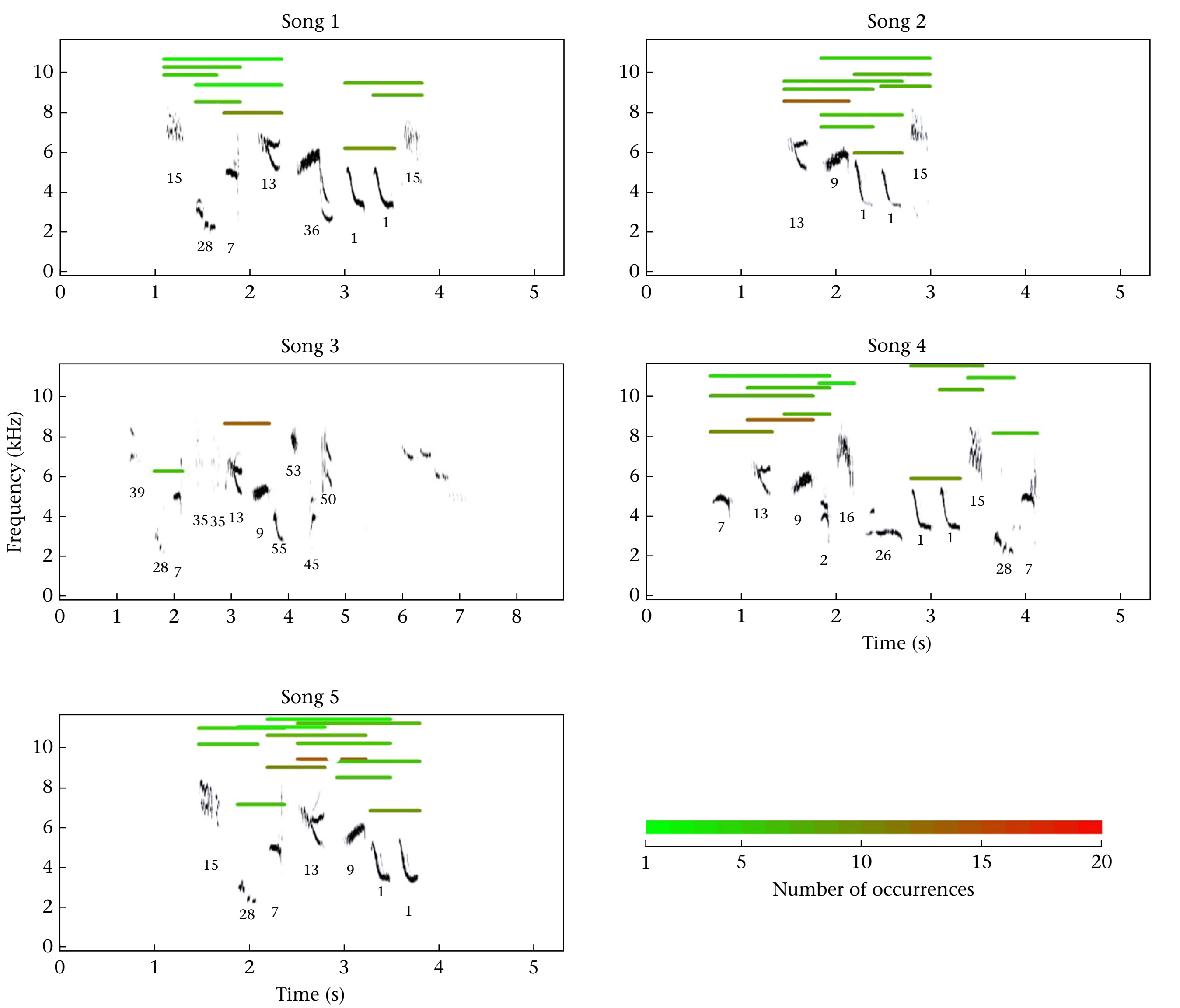

Figure A1. Repeated sequences in the song of the collared flycatcher. Five examples of spectrograms from the same individual. The ID of the syllables is indicated with numbers under the syllables. The repeated sequences with lengths of two, three and four syllables are indicated with lines above the syllables, while the colour of the lines indicates the number of songs in which the given repeated sequence occurred (i.e. number of occurrences).

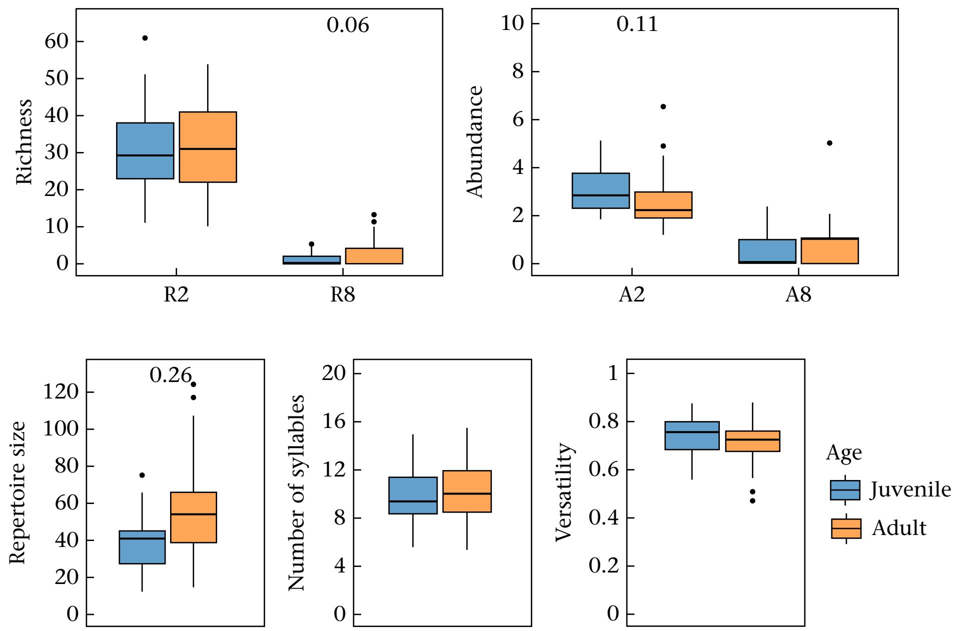

Figure A2. The effect of age on the song variables. The numbers after R and A labels specify the length of the repeated sequence. The effect sizes obtained from the GLMM are shown when the confidence intervals of the estimated effects do not contain 0.

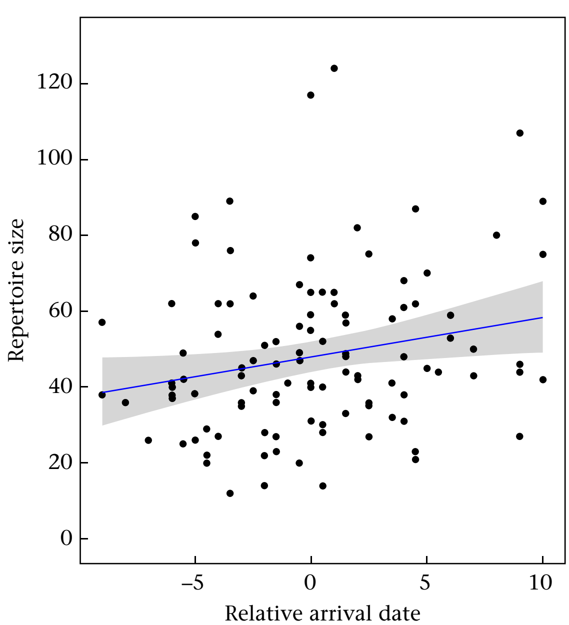

Figure A3. The effect of arrival on the repertoire size. The relative arrival date is calculated as the date of the experiment minus the median of the arrival dates of the males in the given year. The points represent the individuals (N = 109).