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Behavioral Ecology of Elliot's Laughingthrush (*Trochalopteron* (*Garrulax*) *elliotii*, Timaliidae, Aves): 2. Vocal Repertoire

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Abstract—Our work is the first study on the vocal repertoire of one of the babbler species, Elliot's laughingthrush. Field studies were carried out in Hupingshan Nature Reserve, Hunan Province, China. There are three types of signals in the repertoire: songs, calls (chattering), and duets. Songs and calls are used by both males and females. The song consists of a quiet introduction (short note) and a louder main part (two or three tonal notes). There are up to four song variants in the repertoire of a given pair. All songs can be classified into three types. Types I and II represent songs with the main part consisting of three notes, while type III consists of two notes. Types I and II differ from each other in certain features of the frequency modulation shape of the first two notes. All song types can be used during the spontaneous vocalization of a single bird. However, their usage in other contexts differs. Songs of types I and II are more often uttered during vocal interactions of neighbor males. Songs of type III appear to be characteristic of male–female duets. Chattering (calls) is a continuous series of broadband notes. There are several (two to five) note variants in each series. Chattering can be used both during a male–female interaction and as an alarm call. We found an inverse correlation between (1) the duration of pauses between notes, and (2) the number of note variants ("repertoire size") in a series. Both parameters probably reflect the internal state of an individual at a given moment.

Keywords: babbler, song, call, duets

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INTRODUCTION

In Communication 1, we discussed the basic features of breeding, habitat, and social behavior of Elliot's laughingthrush. The purpose of this, second report is analysis of the structure and organization of the definitive vocal repertoire of this babbler species (Timaliidae s. l.). The fact is that the data on the vocalization of this group are very scanty. There are only a few studies specially dedicated to the vocalization of Asian babblers (Gerhard and Thielcke, 1969; Mays et al., 2006; Shief, 2004; Tu and Severinghaus, 2004). Thus, with few exceptions, the vocalization of the majority of species is known only in very general terms. We mean primarily the descriptions given in reference books (MacKinnon and Phillipps, 2013; Martens and Eck, 1995; Robson, 2011; Rasmussen and Anderton, 2005). Therefore, our data on the vocalization of one of the species of babblers, Elliot's laughingthrush (*Trochalopteron elliotii*), are of particular interest not only in terms of describing the vocal repertoire of a new species but also in connection with the studies of communication of birds in general. The fact is that even a cursory acquaintance with this species reveals a number of interesting features. Firstly, there are the duets of males and females. Secondly, the peculiar (compared to the more comprehensively studied temperate species) vocal countersinging of neighbors representing a short series of songs. Finally, thirdly, chattering (calls) is a sequence of several different variants of notes and is performed in many situations. The differences between calls used in different contexts consist in the organization of such a sequence rather than that they are "encoded" by the structure of the constituent notes. For this reason, we believe that the study of vocalizations of this species (and related species) is of theoretical interest. Possible directions of further studies will be considered in the Discussion section. This study, which is largely descriptive, may serve as a starting point.

MATERIALS AND METHODS

Field research. The material was collected in Hupingshan Nature Reserve, situated in the northern part of Hunan province (China). The fieldwork was conducted from April 27 to June 22, 2014. Our plot (Ding-

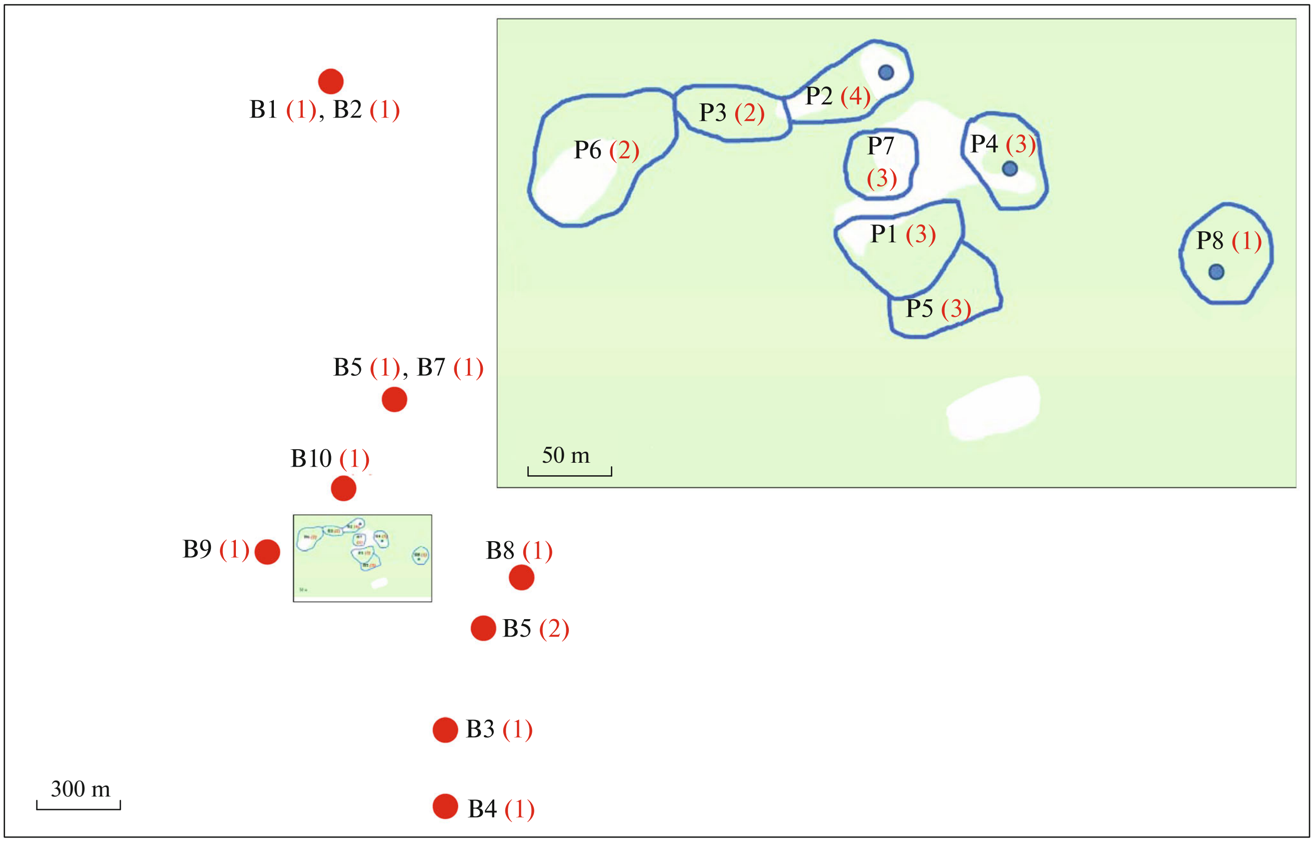

Fig. 1. Points of records of laughingthrushes within (pairs P1–P8) and beyond (B1–B10) the control site. For the control site, territories of different pairs is shown (for details, see Communication 1). In some cases, at one point beyond the site we simultaneously recorded more than one bird (e.g., B1 and B2). The numbers in parentheses indicate the number of song variants recorded from a given pair (within the control site) or from a given individual (beyond the control site).

ping Station, 30°02′ N, 110°31′ E) was located in the northwestern part of the reserve, at an altitude of 1800 m above sea level. The main recordings of laughingthrushes were made at the control plot. The control plot was inhabited by eight pairs of these birds, which were subjects of regular observations (see Communication 1). Two of them (male and female from different pairs) were caught and banded for individual identification with colored plastic rings and painted with theatrical makeup. Observations at the control plot were performed on a regular basis. When recording songs, we attempted to record different songs of a given pair in order to assess the variability of their repertoire most comprehensively. In addition, the vocalization of laughingthrushes was recorded during excursions to surrounding areas. The points of records and the number of phonograms from each of them are shown in Fig. 1; we assumed that each point corresponds to an individual pair of laughingthrushes. In all cases, we tracked birds visually and recorded the adults. More detailed information about these individuals (whether or not they bred, etc.) is missing.

To record the sounds uttered by Elliot's laughingthrush, we used a Marantz PMD-660 tape recorder and a Sennheiser ME66 microphone with a K6 preamplifier. Visualization and processing of records were performed using the Syrinx software. In constructing the spectrograms, we used the Blackman window and the length of the fast Fourier transform equal to 256 points.

The following types of vocalization have been distinguished: songs, duets, and calls. The volume of material and the characteristics of the statistical data processing for each of them are given below.

Songs. To study the songs of this species, we analyzed 28 continuous phonograms (=records) with a total duration of approximately 85 min containing 835 songs. The unit of analysis in this study was the song variant—the set of identical songs recorded from the same individual (Catchpole and Slater, 2008). In our case, usually one song variant was present in only one phonogram. In addition, four of 28 phonograms contained songs of more than one bird (three birds in one phonogram and two in three other phonograms). In addition, in two cases we have two times recorded identical variants in the same place, which suggests that they were obtained from the same bird. Here, two "pairs" of records are involved; i.e., in total in the four phonograms there were two variants of songs. Thus, our final sample included 31 song variants.

For 30 of the 31 variants, more than one song was recorded. For each of these 30 song variants, we measured, when possible, ten songs (on average, 9.6), in total 287 songs. In each song, the introduction (one, rarely two tonal notes) and the main part (two or three tonal notes) can be distinguished. The main difference between them is that the introduction is uttered much more quietly than the main part. For this reason, in part of the phonograms it is difficult to measure correctly the time-and-frequency parameters of the introduction: they were measured for only 22 variants (in total, 217 songs). For each note of the introduction and the main part, the following parameters were measured: (1) the note duration, (2) the maximum fundamental frequency of a note, (3) the minimum fundamental frequency of a note, (4) the frequency modulation (the difference between the maximum and minimum frequencies), (5) the initial frequency of a note, and (6) the final frequency of a note. We also measured the pauses between successive notes and the duration of the main part and the introduction of the song. The time–frequency parameters were measured with an accuracy of 5 ms and 0.01 kHz, respectively.

On the basis of the results of measurements of the time–frequency parameters of notes of different variants of songs, we performed principal component analysis (PCA). For further analysis, we used the factors whose eigenvalues were greater than 1 (otherwise, factors have a smaller explanatory power than the initial parameters). Then, we performed standard discriminant analysis using the values of these factors as variables. Next, when comparing the results of the statistical and a priori classification (i.e., for variants), the calculated Mahalanobis distances were used to calculate the percentage of correct attribution of a given song to the respective variant. Discriminant analysis has shown (see Results) that the studied time–frequency parameters of notes constituting the song make it possible to reliably differentiate different song variants.

At the next step, we took the average values of all note parameters of the main part for each song variant. For the 30 song variants, the average values were calculated for the same parameters and the same sample that was used for the principal component analysis (see above). For one of 31 variants, there was a record of only one song, and we used the results of its measurements. The main part of Elliot's laughingthrush song may consist of two or three notes (see Results). If a song contained two notes, in this analysis we assumed that it lacks a third note (i.e., the values of all parameters for this third note were zero). The variety of song variants of Elliot's laughingthrush was categorized using cluster analysis. The similarities/differences of different song variants were characterized using the Euclidean distance. When constructing the dendrogram, the unweighted pair group method with arithmetic mean (UPGMA) method was used.

Duets. In some cases, a song may be performed in duets. A duet is the song of one laughingthrush (presumably male (see Results)) and notes specific for the duet (not occurring in other cases) produced by another bird (presumably female). Hereinafter, we will call the last type of vocalization the duet notes. To describe duets, we used some of those phonograms that have already been used in the previous step in the study of songs. In total, we had seven phonograms of duets of six different pairs (according to the points of records, see Fig. 1). However, the time–frequency parameters of the duet notes were measured for only five of them: two records of pair P2 were excluded because of their low quality.

Duet notes are one to three identical tonal notes immediately following the song and partially overlapping with it (see Results.). For each such group of duet notes, we measured only the first note by the following parameters: (1) duration, (2) the maximum fundamental frequency of a note, (3) the minimum fundamental frequency of a note, and (4) the frequency modulation (the difference between the maximum and minimum frequencies). In total, we measured 38 notes, from 3 to 10 (on average, 7.6) for each of the five pairs (=five different phonograms). In addition, for the same 38 duets of five different pairs (for which the first duet note was measured), we estimated (in %) the degree of overlapping of vocalizations of different birds. For this purpose, we measured a part of the song of one bird and the duet notes of the other bird that overlap in time with the partner. These values were compared with (1) the duration of the song of the first bird and (2) the duration of duet notes of the second birds, from the beginning of the first note to the end of the last one.

We also measured the pauses between successive duet notes (if there were more than one): a total of 56 pauses, from 6 to 17 (on average, 11.2) for each of the five pairs.

Calls. We analyzed eight phonograms (belonging, judging by the localities of records, to different individuals (Fig. 1)) of these vocalizations with a total duration of 13 min. In total, they contained 479 notes (on average, 60 ± 33 notes in each phonogram). In this sample, 26 variants of calls were distinguished. The call variant is a set of identical notes of an individual (i.e., in our case, present in the same phonogram). To describe the time–frequency parameters, we measured one note of each variant. Such a small sample size is determined by the fact that our task was only to define the limits of variability of different parameters. We measured (1) the minimum fundamental frequency of a note, (2) the maximum fundamental frequency of a note, (3) the duration, and (4) the frequency modulation period (the duration of a note divided by the number of frequency peaks in it). The

Table 1. Time–frequency parameters of the notes in the introduction. The asterisks show the parameters of the introduction that were significantly different in the disyllabic and trisyllabic songs (Student's *t* test)

Parameter	Disyllabic songs (n = 80)		Trisyllabic songs (n = 137)	
	mean ± SD	min–max	mean ± SD	min–max
Duration	65 ± 25	25–140	70 ± 20	35–110
Freq. max, kHz*	3.06 ± 0.28	2.73–3.78	3.42 ± 0.67	2.37–5.31
Freq. min, kHz*	1.53 ± 0.28	0.99–2.35	1.77 ± 0.24	1.24–2.4
Freq. mod., kHz	1.52 ± 0.32	0.81–2.53	1.64 ± 0.64	0.69–3.66
Freq. init., kHz*	1.71 ± 0.23	1.08–2.37	2.18 ± 0.64	1.53–3.79
Freq. fin., kHz	2.76 ± 0.25	2.16–3.21	2.48 ± 0.18	1.95–2.88
Pause, ms	130 ± 60	10–260	115 ± 55	10–190

Duration, duration of a note; Freq. max., maximum fundamental frequency of a note; Freq. min., minimum fundamental frequency of a note; Freq. mod., frequency modulation (difference between the maximum and minimum frequencies); Freq. init., initial frequency of a note; Freq. fin., final frequency of a note; Pause, duration of the pause between the note of the introduction and the main part of the song.

time–frequency parameters were measured with an accuracy of 10 ms and 0.1 kHz, respectively (the lower, compared to songs, accuracy of measurements was due to the lower quality of records).

Statistical data processing was performed using the Statistica 6.0 software. The examined samples had a normal distribution (Kolmogorov–Smirnov test, $p > 0.05$). For this reason, we used the parametric tests. In addition to the methods described above, we used Student's *t* test and the χ-square test. In the case of a small sample size, we used the nonparametric methods (Spearman rank correlation and Kruskal–Wallis test).

RESULTS

Songs

Laughingthrushes sing songs in series, or vocal episodes. Each episode is separated from the next one by a long pause (usually tens of minutes). Episodes are not very long. For example, the studied phonograms contained, on average, 23.8 songs of the same variant (max 59, n = 30), and the duration of these records was, on average, 2 min 36 s (maximum 5 min 34 s, n = 28). During recording of the songs of Elliot's laughingthrush, a series in most cases was not recorded from the very beginning, but the recording was stopped when the bird stopped vocalizing. Thus, the presented numbers give an idea about a certain average minimum duration of vocal episodes (series). With regard to the maximum duration, we once heard a series that lasted for 13 min (it was not recorded). The duration of pauses between successive songs in a series (episode vocal) is, on average, 4.3 ± 2.2 s (range, 1.7–16.9 s, n = 496).

The song of Elliot's laughingthrush is a short (approximately 1 s long) acoustic structure consisting of several tonal notes that are usually modulated in frequency. In each song, the introduction and the main part can be distinguished (Fig. 2). The introduction consists of one (rarely two) short notes uttered more quietly than the main part of the song and separated from it by a pause, usually (but not always) longer than the pause between the tones in the main part. The main part of the song consists of two or three tonal notes. Hereinafter, the songs whose main part consists of two and three notes will be called "disyllabic" and "trisyllabic," respectively. Interestingly, the duration of the main part in disyllabic and trisyllabic songs does not differ ($p = 0.68$ according to Student's *t* test), since the former consist of generally longer tones (Table 2). In addition to the differences in the number of notes in the main part, disyllabic and trisyllabic songs differ in the introduction. The notes that are used in the introduction to the disyllabic songs are in a more low-frequency range as compared to those that precede the trisyllabic songs (Table 1). Out of the 31 variants of songs in our sample, 10 were dissyllabic and 21 were trisyllabic.

Principal component analysis was performed using ten variants of the disyllabic songs. For the analysis, we used the time–frequency parameters shown in Table 2. The analysis revealed three factors (with eigenvalues 4.5, 3.8, and 2.1), which summarily explained 80.8% of the variability. The discriminant analysis of these factors showed that all variants of songs were statistically clearly distinguishable: the correct attribution accounted for 93.3% (Wilks lambda 0.00006, $p \ll 0.0001$, $n = 90$). A similar principal component analysis of the trisyllabic songs (a total of 21 variants) revealed three factors (with eigenvalues 8.7, 3.1, and 2.7) describing 72.6% of the variability. The results of the discriminant analysis of these factors are as follows: correct attribution 90.4%, Wilks lambda 0.00005, $p \ll 0.0001$, n = 197. Thus, different variants of both disyllabic and trisyllabic songs are clearly distinguishable. This allowed us to use each song variant as an independent variable in the cluster analysis.

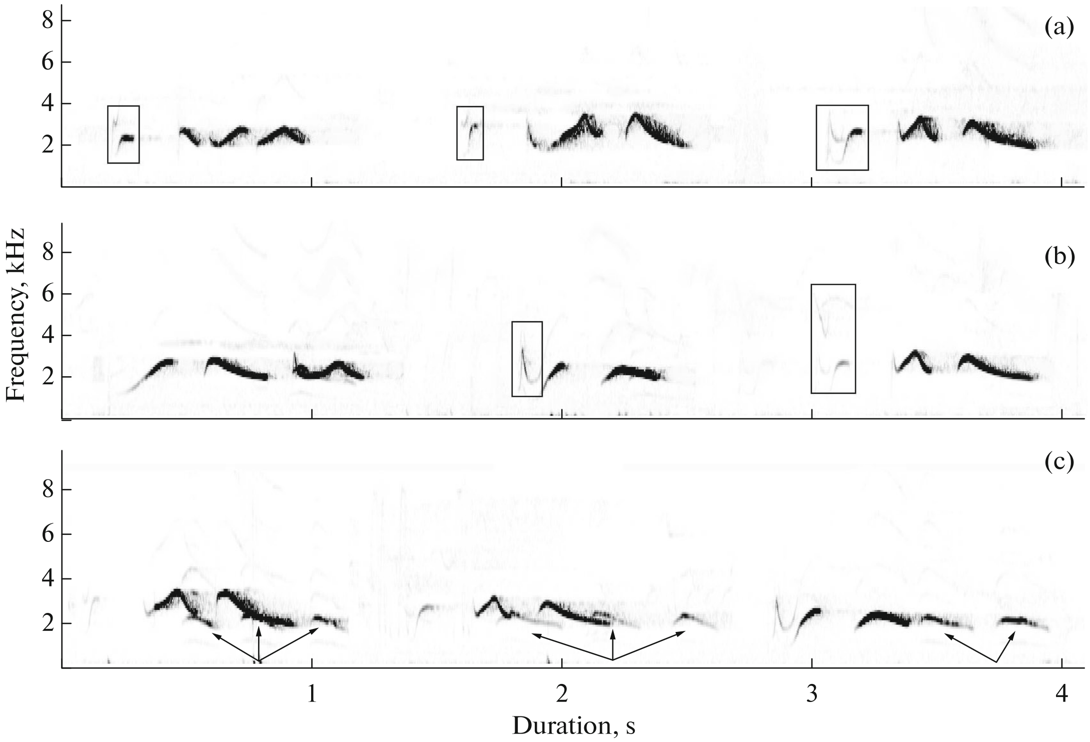

Fig. 2. Examples of songs repertoires pairs P1 (a) and P4 (b), in the framework allocated in introduction. In, examples of duets of pairs P5, P7, and P4 (left to right), duet notes are indicated by arrows (connected arrows are the note of a single individual).

The cluster analysis showed that all the variants of songs can be divided into three types (I, II, and III) (Fig. 3). Type III included the disyllabic songs, and types I and II included the trisyllabic songs. The last two types differed in the characteristics of the frequency modulation of the first two notes. In type I, the first note is "bottom–up" in frequency (Freq. init. < Freq. fin.), and the second note is "top–down" (Freq. init. > Freq. fin.). In type II, the situation with the notes was the opposite. Below (section *Context-Specificity of Different Types of Songs*), we will consider some differences in the use of different types of songs.

Observations in the control site make it possible to estimate the size of the repertoire of different pairs. The individual territories of pairs of laughingthrushes are small (see Communication 1). We watched the birds for a long time (the total duration of field research was approximately two months), noting the territorial interactions or recoding simultaneously members of different pairs. On this basis, we could determine (though with some caution) to which pair a given individual belonged proceeding from the fact where it was located. Our fragmentary observations indicate that songs can be performed not only by males but also by females (data for two tagged birds). The majority of birds were not distinguished individually. For this reason, when recording the singing of laughingthrushes at a given point, we could only determine to which pair a given bird most likely belonged, but its sex remained undetermined. For this reason, hereinafter we will consider the repertoire of one pair (male + female) rather than the repertoire of one individual.

The repertoire of each pair included several variants of songs. In the control plot, we recorded one to four variants of songs from each pair (median 3, n = 8 pairs). We compared the variety of song variants in the repertoire of one pair with their total variety in the population. For this purpose, the distribution of song variants in the repertoire of a given pair with respect to the distinguished song types was considered (see Fig. 3). We used the data for only five pairs, for each of which three or four song variants were recorded (Table 3). The repertoires of two of the five pairs included songs of all types distinguished (I–III), and the remainder included two songs of the three possible types. In all cases, the distribution did not differ from the uniform distribution of song variants of a given pair with respect to all types of songs (χ-square test, $p > 0.05$). On this basis, it can be concluded that the repertoire of one pair, apparently, includes songs of all three types distinguished by us.

The structure of a given variant of song of a given individual, most likely, is stable over time. This is evidenced by our fragmentary materials. In two cases, we recorded identical songs to our hearing at intervals of 17 and 20 days in the same place, i.e., presumably from the same birds (two different individuals are in question). In each case, differences for any of the time–frequency

Table 2. Frequency–time parameters of the notes constituting the songs and the temporal parameters of songs

Parameter	Disyllabic songs ($n = 90$)		Trisyllabic songs ($n = 197$)	
	mean ± SD	min–max	mean ± SD	min–max
Durat. tot., ms	495 ± 110	260–660	500 ± 125	290–790
Durat. 1, ms	210 ± 70	70–335	120 ± 50	30–235
Freq. max. 1, kHz	3.34 ± 0.16	2.88–3.66	3.02 ± 0.37	2.47–4.67
Freq. min. 1, kHz	1.89 ± 0.37	0.84–2.25	1.78 ± 0.39	0.92–2.94
Freq. mod. 1, kHz	1.44 ± 0.45	0.72–2.61	1.23 ± 0.52	0.5–3.68
Freq. init. 1, kHz	2.58 ± 0.62	1.32–3.28	2.02 ± 0.50	1.17–3.26
Freq. fin. 1, kHz	2.54 ± 0.15	2.13–2.94	2.57 ± 0.31	1.95–3.28
Pause (1–2), ms	80 ± 30	20–135	80 ± 45	15–310
Durat. 2, ms	290 ± 50	185–380	155 ± 45	75–275
Freq. max. 2, kHz	3.17 ± 0.28	2.46–3.60	3.05 ± 0.27	2.42–3.72
Freq. min. 2, kHz	1.79 ± 0.13	1.41–2.30	1.98 ± 0.31	1.32–2.82
Freq. mod. 2, kHz	1.38 ± 0.26	0.72–1.78	1.07 ± 0.22	0.61–1.83
Freq. init. 2, kHz	2.32 ± 0.38	1.47–3.08	2.58 ± 0.49	1.79–3.76
Freq. fin. 2, kHz	2.05 ± 0.14	1.67–2.49	2.54 ± 0.46	1.89–3.39
Pause (2–3), ms	–	–	55 ± 25	15–125
Durat. 3, ms	–	–	225 ± 55	145–390
Freq. max. 3, kHz	–	–	3.11 ± 0.23	2.72–3.60
Freq. min. 3, kHz	–	–	1.95 ± 0.22	1.35–2.51
Freq. mod. 3, kHz	–	–	1.16 ± 0.24	0.80–1.86
Freq. init. 3, kHz	–	–	2.44 ± 0.46	1.47–3.40
Freq. fin. 3, kHz	–	–	2.26 ± 0.23	1.82–2.91

Durat. tot., duration of the main part of a song; durat., duration of a note; Freq. max., maximum fundamental frequency of a note; Freq. min., minimum fundamental frequency of a note; Freq. mod., frequency modulation (difference between the maximum and minimum frequencies); Freq. init., initial frequency of a note; Freq. fin., final frequency of a note; Pause (1–2), duration of the pause between the first and second notes in a song; 1–3, sequence numbers of notes in a song (e.g., Freq. max. 2, maximum frequency of the second note, etc.).

parameters of the notes constituting the song were not revealed (Student's t test, $p > 0.05$).

Duets

A duet always starts with the song of the first individual, and then the second bird enters by uttering duet notes (Fig. 2). The duet notes are specific and do not occur in other situations.

Table 3. Distribution of different variants of songs from the repertoires of five pairs with respect to the types of songs distinguished (the number of pluses corresponds to the number of variants of songs of a given pair belonging to the given type)

Pair	Type I	Type II	Type III
P1	++	+	
P2	+	++	+
P4	++		+
P5	+		++
P7	+	+	+

Duet notes are always two or three (in rare cases, one) tonal notes with a duration of 180 ± 40 ms (range, 110–280 ms, $n = 38$). The values of the lower and upper boundaries of the frequency spectrum are 1.9 ± 0.1 (1.7–2.1, $n = 38$) and 2.6 ± 0.3 (2.3–3.4, $n = 38$), respectively. The duration of the pause between successive notes is, on average, 130 ± 30 ms (range, 70–200 ms; $n = 56$).

A characteristic feature of the duets of Elliot's laughingthrush is the overlapping of parts performed by different birds: songs of one bird and duet notes of the other (Fig. 2c). According to our data, the duet notes overlap, on average, 45.5 ± 28.1% (median, 46.9%; range of values, 0–94.5%; $n = 38$) of the main part of the song of the partner. The main part of the song, in turn, overlaps 49.3 ± 30.7% (median, 53.6%; range of values, 0–100%; $n = 38$) of the duet notes. Different duets (in our case, recorded, most likely, from different birds) differ in the degree of overlapping (Kruskal–Wallis test, $p < 0.05$ for both songs and duet

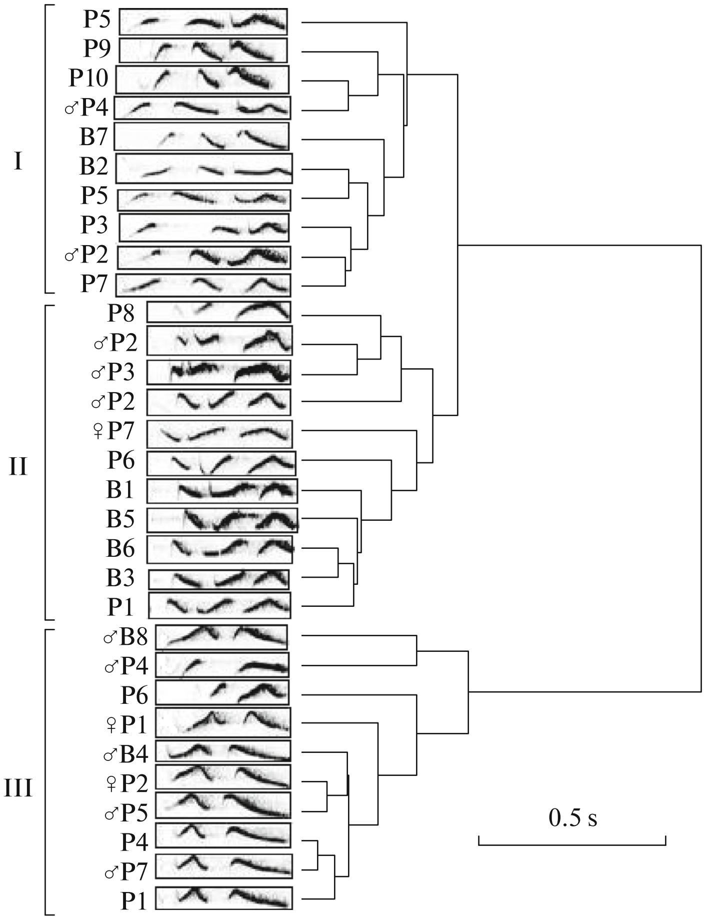

Fig. 3. Dendrogram showing the similarities/differences in different variants of songs of Elliot's laughingthrush. Designations: P, songs of the pairs inhabiting the control site; B, songs of the pairs recorded beyond the control site. The numerals next to the letters correspond to the numbers of pairs. Roman numerals correspond to the three types of songs distinguished by us. Signs "male" and "female" designate the songs of the birds whose sex was either known exactly or assumed on the basis of the fact that one of the birds uttered duet notes before or after this song.

notes). For example, the medians of the overlapping of the song of the first laughingthrush with the duet notes of the second bird may vary from 0 to 78% in different phonograms. Thus, in some cases, the duet is more antiphonal, whereas in other cases it is closer to uniphonal.

Observations of two pairs in which one partner was tagged made it possible to determine the parts of males and females in a duet. In addition, in all cases when we identified a duet (by recording it or "visually"), birds stayed close to each other (within a distance of 1–5 m), without showing signs of aggression. This suggests that the duet vocalization is characteristic of the members of a pair, with the male singing and the female uttering the duet notes.

Context-Specificity of Different Types of Songs

Songs of all three types distinguished by us can be heard during "spontaneous" vocalization of a single individual. In fact, this is the most typical situation. However, two or more birds situated nearby (at a distance of no more than several tens of meters) may vocalize simultaneously (at least one of them sings songs). We observed two types of such situations. The first is the duet described above. The second is the vocal countersinging of birds from neighboring pairs (see also Communication 1). In this case, two or three birds (in the last case, most likely, both the male and the female of the same pair sing) perform songs for several minutes generally in turn, but without a clear consistency. This countersinging lasts for several minutes. Usually one of the birds falls silent first, and then, after performing several more songs, the other does (or the others do). Thus, the completion of the countersinging is, to a certain extent, concerted. This suggests that, in this case, there may be a vocal interaction of laughingthrushes rather than just a random combination of their songs in time.

In the five (of the seven) duets recorded, type III (disyllabic) songs were identified. In the other two duets, belonging to pair P2, a type I song was identi-

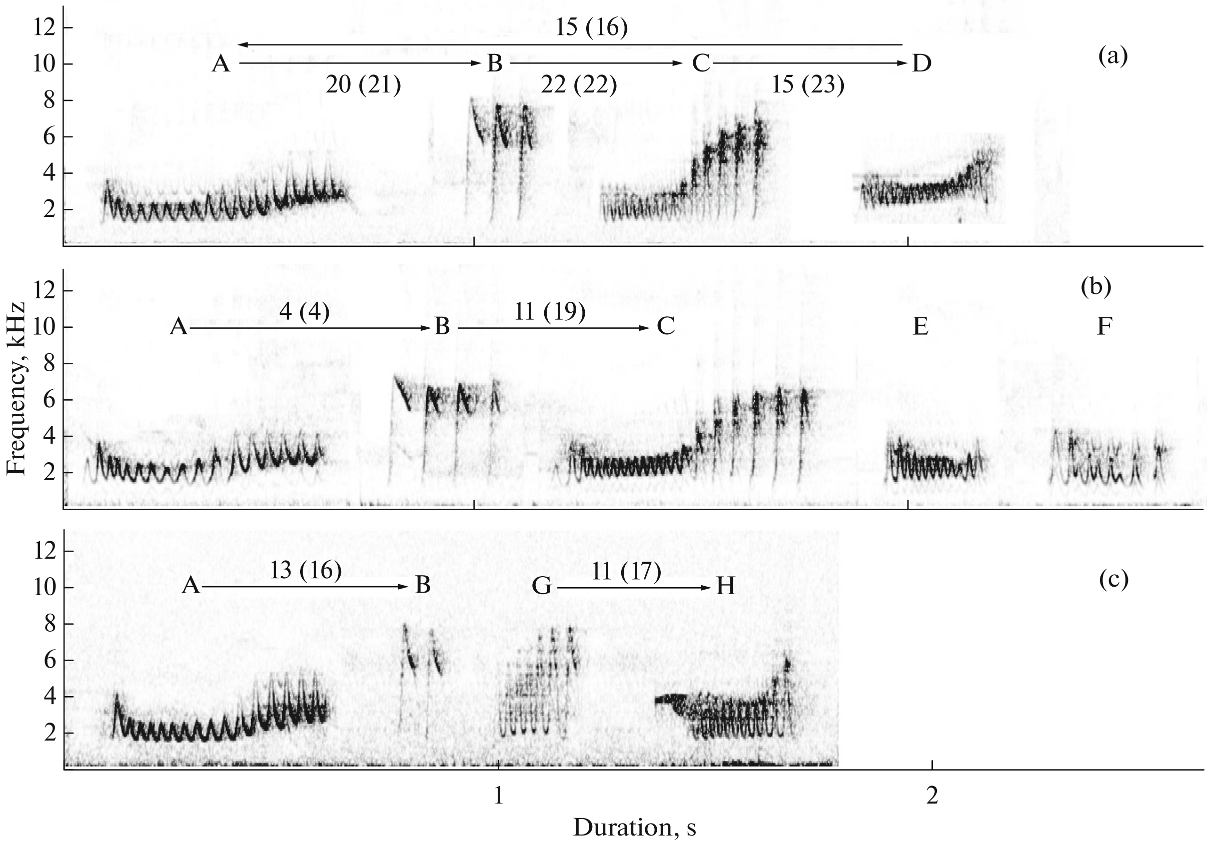

Fig. 4. Catalogues of three phonograms (a–c) of Elliot's laughingthrush calls. Similar calls of different individuals are indicated by the same letters. Arrows indicate the most frequent transitions between the different variants of calls in a given phonogram. The numerals above the arrows show the number of observations of a given transition, the total number of transitions (excluding the repeats of the same notes) is shown in parentheses. Phonograms (a) and (b) were recorded during alarm near the nest, and phonogram (c) was recorded in an unclear situation but in the absence of a nest in the given pair.

fied. Thus, the type III songs are most characteristic of the duets.

In the countersinging, the situation is different: type III songs have not been identified at all. In total, we have phonograms of four countersinging. In one of them, three birds sing—a pair (male and female) and a laughingthrush from a neighboring pair. In the other three phonograms, two individuals (most likely from different pairs) sing. In all cases ($n = 9$ song variants), songs were of types I and II (trisyllabic).

Thus, different types of songs are characterized by a certain contextual specificity. However, our data are insufficient to make final conclusions. It should be noted that songs of types I and II, on the one hand, and type III songs, on the other, are clearly distinguishable aurally. The songs of the first two types, in addition to the introduction, include three notes, whereas type III songs include only two notes.

Chattering (Calls)

Chattering (calls) of Elliot's laughingthrush is a continuous series of relatively low-frequency notes, which are aurally perceived as "chattering" (Fig. 4). The duration of the pauses between successive notes varies widely in different phonograms (see below). The values of this parameter in our sample varied from 30 ms to 26.5 s ($n = 470$), usually falling in the range of 300–400 ms (median of the total sample, 350 ms; $n = 470$). The total duration of a series of calls is usually several minutes; however, this parameter is highly variable.

In each series of calls of one bird, several variants of notes that are repeated in an unchanged form throughout the record can be distinguished. Thus, we can talk about the chattering repertoire of a given laughingthrush. All of these variants are alternated in a single sequence. Apparently, judging by the dependence of note variants in a given series on the context (see below), not ever series of calls of a given individual contains the complete repertoire. Each phonogram of our sample contained two to five (median, 3; $n = 8$) variants of notes. The repertoires of calls identified in three records are shown in Fig. 4.

In our sample of phonograms of calls from eight individuals, we identified a total of 26 variants of notes (the sum of variants of calls from all phonograms). Some of them are very similar in different birds (e.g., the variants designated by the same letters in Fig. 4).

With regard to the spectrum structure, three types of calls can be distinguished. The first, most common (19 out of 26 variants of notes from eight individuals in our sample) is the warbling notes with a well-expressed frequency modulation (A, D, E, F, and H in Fig. 4). The lower boundary of the fundamental frequency is, on average, 1.4 ± 0.2 kHz (median, 1.4 kHz; range, 0.7–1.6 kHz; n = 19), and the upper boundary is 5.1 ± 1.4 kHz (median, 5.1 kHz; range, 2.9–8.0 kHz; $n = 19$). The duration of notes was 270 ± 140 ms (median, 240 ms; range, 50–550 ms, $n = 19$). The average period of frequency modulation was 30 ± 10 ms (median, 20; range, 10–40 ms; $n = 19$). However, the frequency modulation period may vary even within a single note, e.g., gradually increasing or decreasing from its beginning to end (e.g., note G in Fig. 4c).

The second type (4 of 26 variants) includes compact series of short broadband patches with L-shaped frequency modulation. Three of the four notes of this type, uttered by different individuals, are shown in Fig. 3 under the letter B. The frequency range of notes of this type is wider than the previous one. The lower limit of the fundamental frequency is in the range of 1.3–1.6 kHz; the upper, in the range 7.4–8.5 kHz (in both cases, the range of values is given; $n = 4$). The duration of a note varied in the range 100–270 ms ($n = 4$). The number of patches in the series (single note) is usually 2–5.

Finally, the third type (3 of 26 variants) includes composite notes representing an end-to-end association (without a pause) of notes of the two previous types. An example is note C in Figs. 4a and 4b. The range of variability of the time–frequency parameters of the considered notes ($n = 3$) is as follows: the lower and upper boundary of the fundamental frequency is 1.1–1.5 kHz and 6.5–7.5 kHz, respectively, and the duration is 370–580 ms.

Because different variants of notes alternate in one sequence, we can talk about the syntax of chattering sequences. The most common practice is that a bird produces variants of notes present in a given series of notes in a linear sequence and then starts all over again. For six recordings (containing three or more variants of calls), the median values of linearity and constancy indices were 0.50 (range, 0.38–0.75) and 0.78 (range, 0.62–0.93), respectively. Thus, each given note variant with a high probability is followed by a strictly defined other variant. In addition, the same notes may often be repeated several (two or three) times.

In our sample of eight phonograms of calls, two were recorded when adult birds were alarm calling near a nest with a clutch, and others were recorded during within-pairn interaction or during a territorial conflict. It was found that, when alarm calling near a nest, babblers utter a series of calls having (1) the largest number of note variants (note variants repertoire size) and (2) the shortest duration of pauses between successive notes (phonograms are indicated by arrows in Fig. 4). Moreover, the parameters mentioned were negatively correlated for the entire sample (Fig. 5).

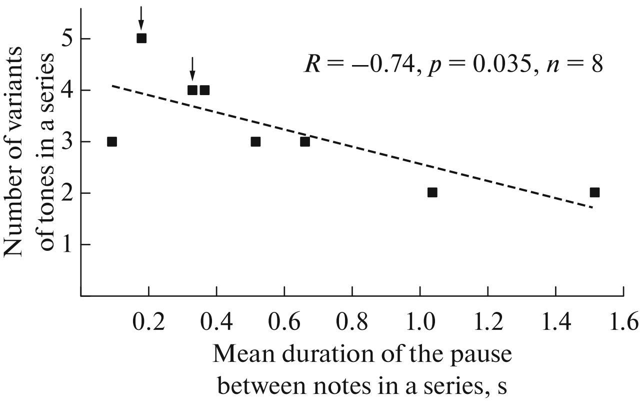

Fig. 5. Correlation between the number of variants of notes in a series of calls ("repertoire size") and the median of the duration of the pause between successive notes in a given recording. The Spearman correlation coefficient is given. Each point corresponds to one phonogram. The arrow marks the recordings made when laughingthrushes were worrying near the nest in the presence of the observer.

DISCUSSION

In this article, we presented data on Elliot's laughingthrush vocalization. In our opinion, this is a sufficiently comprehensive description of the definitive repertoire, although some rare notes might have been missed. The features of songs, duets, and calls are sequentially discussed below.

Songs. The song of Elliot's laughingthrush is a short sequence of several tonal notes. Members of both sexes sing, but males do it much more often. Only in three cases (in three different pairs) did we definitely record singing females. In other cases, songs belonged to either a male or a bird the sex of which was not defined. Visual comparison of the phonograms of songs belonging to males or females (shown in Fig. 2) showed no clear distinctions, although the available data are insufficient. The songs of females are very similar to some of the songs of males. The repertoire of each pair (male + female) and, apparently, of each individual includes several (according to our data, up to four) song variants. This estimate of the maximum repertoire corresponds to our impression from observing the laughingthrushes in the control plot (see Fig. 1), where we had the opportunity to hear them almost daily. For two months of work here, we did not record songs that were different by ear from those that were recorded and used in this work.

Most likely, the structure of a given song variant of a given individual is stable over time. This suggests individuality in the song structure.

The entire variety of the songs recorded by us was divided into three types (see above). Of great interest is the revealed trend to use different types of songs in different contexts. It was found that, in the countersinging of babblers from neighboring pairs ("territorial context"), the trisyllabic songs (types I and II) are commonly used, whereas in duets in which the male and female of a pair are presumably involved (see below), disyllabic songs (type III) are primarily used. Thus, in duets, laughingthrushes use songs of only one type, whereas in the countersinging of neighbors, songs of two types are used; that is, the variety of songs that are used in the last situation is greater. It is unclear as yet whether there are more subtle functional differences between the songs of types I and II.

Published data indicate that, in some species (e.g., the New World warblers of the family Parulidae), different types of songs are used in different contexts and, therefore, may have different function. However, these data are not indisputable (for a review, see Opaev, 2012). They are also not indisputable in the case of Elliot's laughingthrush, in particular, due to the scarcity of data. However, for other species of birds, we could not find evidence that different types of songs of males can be used, on the one hand, during territorial conflicts and, on the other hand, in duets with females.

Duets of birds have drawn the attention of many researchers (for a review, see Hall, 2004). However, many features of this type of vocalization are not yet well understood. In particular, there is no clear understanding of the function of duets. Possibly, one reason for this lies in the fact that the structure of duet vocalizations and the characteristics of using duets vary in different species. Thus, in our view, it is incorrectly to speak of a certain single function of duets in birds in general. Below we will consider our data on the duet vocalization of Elliot's laughingthrush.

First of all, we assume with high probability that duets are characteristic of a pair (male + female). Single observations of marked birds made it possible to determine the parts of each of the partners. In duets, one of the birds (most likely, the male) performs songs (primarily disyllabic), whereas the second bird (female) utters specific duet notes. The duet notes always follow the song, often overlapping with its final part. Songs can be also performed in other situations, the most common of which is the vocalization of a single individual. On this basis, we propose the following scheme. The male begins to sing. If the female is nearby, she may accept or reject the "invitation" of the male, i.e., to respond or not to respond to him with duet notes (usually in duets the female is not far from the male).

Now consider the data on the contextual confinement and seasonal dynamics of the occurrence of duets, presented in Communication 1. Our observations indicate that duets are more commonly observed at the beginning of the breeding season until the appearance of nests. In addition, duets accompanied the only mating episode of Elliot's laughingthrushes observed by us. These data are consistent with one of the hypotheses about the functions of duets. According to this concept, a duet may implement the function of synchronization and mutual stimulation of partners before breeding (Kunkel, 1974). Indeed, the most important prediction of this hypothesis is the fact that duets are observed before the appearance of a nest and are not typical afterwards. By the way, this hypothesis does not fully explain the function of duets in the majority of species, because in many of them duets are not strongly confined to the beginning of breeding (Farabaugh, 1982). Nevertheless, it cannot be ruled out that, in Elliot's laughingthrush, duets serve for mutual stimulation of partners. Something similar is expected for some other species. For example, the slate-colored boubous (*Laniarius funebris*) more readily respond to the solo of a partner at the beginning of the breeding season rather than at the end of it (Sonnenschein and Reyer, 1983). A similar situation is observed in Elliot's laughingthrush.

Chattering (calls). The organization of series of calls in Elliot's laughingthrush is unusual. In the majority of passerine species, each particular series of calls is composed of notes of only one or two types. Such series may be confined to specific situations, e.g., alarm calls (for a review, see Marler, 2004, 2006). Therefore, we can talk about the situational specificity of different types of calls. In Elliot's laughingthrush, in fact, the same notes can be used in different situations (namely, during the interaction of members of a pair, territorial conflicts, and in alarm near the nest). In addition, in the species of interest, each series of calls includes several variants of notes. The available fragmentary data indicate that the structure and organization of a series of calls may vary depending on the context. In particular, in a series of calls performed in alarm near the nest, (1) the pauses between successive notes are reduced and (2) the number of variants of notes in series ("repertoire size") is reduced. Thus, in this case, some important information may be provided not only by the structure of notes as such but also by the organization of the sequence of notes. It can be assumed that, with increasing expression of birds, the sequences of calls produced by them become "denser" (the pauses between notes are reduced), and the number of variants of notes in them (the "repertoire size") increases. Indeed, in our opinion, laughingthrushes behave most emotionally when they call the observer near the nest, whereas territorial conflicts, for example, proceed much less expressively (see Communication 1).

Similar examples are known in the literature, but they are scanty. For example, in the tits of the genus *Poecile*, the repertoire includes complex calls, each of which consists of several note types. The organization of such notes into a whole call obeys a linear syntax—the principle ABCD, ABCCD, ABBC, etc. (Ficken et al., 1978; Ficken and Popp, 1992). For these species, the dependence of the structure of such complex calls on the behavioral context was shown (Freeberg and Lucas, 2002; Templeton et al., 2005). This may also be applicable to Elliot's laughingthrush (see above). Further studies of this species may refine and extend these findings.

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