Structure of Territorial Songs in the Japanese Bush Warbler (Cettia diphone)

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Abstract Songs of male Japanese Bush Warblers were tape-recorded and the structure of their songs were analyzed. The song, which was notably low in pitch (about 700 Hz in the lowest part), consisted of the initial CF (Constant Frequency) part (introductory whistle) and the FM (Frequency Modulated) part. There were two basic song types, which were named type-H song and type-L song. The CF part of the type-H song was one continuous whistle, whereas that of the type-L song consisted of several short whistles of the same frequency. Type-H songs had a wider frequency range, louder, longer and had more complex structure than type-L songs. Each male had 2 to 5 different patterns of these type-H and type-L songs with an average of 2.8 songs, and had at least one type-H and one type-L song. The songs in the repertoire of each male formed a gradation in terms of frequency range, loudness and structural complexity. When singing, males tended to avoid the repetition of the same song type, and the time interval between successive two songs tended to be highly variable. Also, in successive renditions of the same song pattern, the absolute frequency of the CF part varied each time within a certain frequency range, but the FM part was always repeated with high stereotypy. These singing patterns might be adaptations for the long-range communication in the bushy habitat that the species lives in.

Key words Vocalization, Auditory communication, Signal structure, Aves, Passeriformes, Sylviidae

Introduction

Many bird species rely on vocalization as a primary channel for their communication (Smith 1982). This is particularly true in species that live in an environment where communication through visual channel is difficult or impossible. One such environment is the dense undergrowth of the temperate deciduous forest. This particular environment poses difficulty on vocal communication too, because the dense foliage and bush hinders transmission of audio signals by attenuating and reflecting sound. It is, therefore, natural for us to expect the bush-living bird species to have some highly developed vocal communication system.

The Japanese Bush Warbler, *Cettia diphone*, is a species that inhabit this kind of bushy habitat in Japan. It is common in secondary forests with dense undergrowth, typically small bamboo of the genus *Sasa*. In the central island of Honshu, the males arrive at the breeding ground in early spring and form exclusive territories, and sing rather unusual songs in them. Males do not help females in incubation and in feeding nestling (Haneda & Okabe 1970). This paper describes the structure of the Japanese Bush Warbler's song, as well as the temporal and sequential patterning of the singing behaviour.

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Materials and Methods

Field recordings were made during four breeding seasons at three locations in Japan: Haccho-daira (Kyoto prefecture, 35°14′ N, 135°50′ E, Alt. 810m) in 1982, Kayano-daira (Nagano prefecture, 36°50′ N, 138°30′ E, Alt. 1460m) in 1983 and 1984, Togakushi (Nagano prefecture, 35°45′ N, 138°05′ E, Alt. 1220m) in 1984 and 1985. In total, 12,384 songs were recorded from 149 birds. Eighty-five of these birds were captured before the recording had started, measured and marked with unique combinations of plastic colour rings. Songs were recorded using a Victor MU-510 shotgun microphone connected to a channel of Sony WM-D6 stereo cassette tape recorder. During the recording, the observer verbally recorded the position of the bird, its behaviour and other data simultaneously with a small microphone connected to the other channel of the tape recorder.

For laboratory recording of the songs, three adult males were captured at Sugi-touge (Kyoto prefecture, 35°09′ N, 135°48′ E, Alt. 820m) on 6 December 1981 using mist nets. They were kept for 5 weeks in the laboratory under short day photoperiod (11L-13D) and then induced to sing by exposing them under long day photoperiod (14L-10D). Recordings began two weeks after they had started singing. Their songs were recorded using a Sony TC-D5M cassette tape recorder and a Sony ECM-150 microphone.

Recorded songs were analyzed in several ways. Firstly, tape-recorded songs were converted to 12 bit digital data at the sampling speed of 10 kHz using FACOM M-382 computer system at Kyoto University Data Processing Center. Data were analyzed using software written by the author. The purpose of this analysis was to measure the absolute frequency of the introductory whistle note(s) (the CF part of the song) using 1024 point FFT. The precision of frequency measurement was about 9.56 Hz.

Secondly, the songs were analyzed with KAY-7800 Sonagraph with 150 Hz filter bandwidth and 0 to 8 kHz frequency range setting. Repertoire of each bird was determined by visual inspection of the sonograms.

Thirdly, and later, the entire system was moved to a software system written by the author ('Sonogram') running on the NeXT workstation, and the recorded sounds were converted to 44 kHz, 16 bit digital data. Using this system, the time-frequency structure of songs were analyzed by directly measuring the sonograms (time-frequency), spectrograms (frequency-amplitude) and waveforms (time-amplitude) displayed on a monitor using a mouse-controlled cursor.

Fourthly, the amplitude (SPL) of songs was analyzed using a continuous bout of 30 songs recorded at Togakushi on June 20, 1985. During this recording, the bird was sitting on the same perch 2m above the microphone. This particular recording was chosen because the bird was very close to the microphone. Thus, the ground effect and other causes of frequency dependent attenuation were almost negligible and amplitude values obtained were thought to be parallel with the source amplitude. The analysis was done at Rockefeller University Field Research Center using 'Signal' program (coded by Kim Beeman) running on Dec PDP11/23 minicomputer. SPL was determined by measuring root mean square voltage values of four 100 ms signal blocks taken from each of the last four notes of the song. Obtained values were later converted into decibel values.

Results

Song type

In all birds studied, the song consisted of an initial CF (constant frequency) part followed by a FM (frequency modulated) part (Fig.1). There were two basic types of songs in the repertoire of each male, which were named type-H and type-L songs respectively. In type-L songs, the CF part was broken up into a series of several notes of the same frequency, and in type-H songs, the CF part was a continuous whistle. If a bird had more than one type-L or type-H songs, they were named H1, H2, H3 and so on. The numbers were attached according to the descending order of their relative CF frequencies, H1 being the highest of all type-H songs. The CF frequencies of different song types in a male's repertoire showed little overlap as shown later, and type-H songs had higher CF frequencies than type-L songs without exception.

Repertoire size

Each male had a repertoire consisting of 2 to 5 (2.8 in average) different FM patterns (song types). The distribution of repertoire size among males is shown in Fig. 2. All birds had at least one type-H song and one type-L song.

CF frequency and FM pattern

Parameters used for the measurement are shown in Fig. 3. The summary of the measurement results is shown in the Table 1. The type-H song had higher values in all the parameters ($P < 0.0001$, Mann-Whitney U-test) except FM_Min (the minimum FM fre-

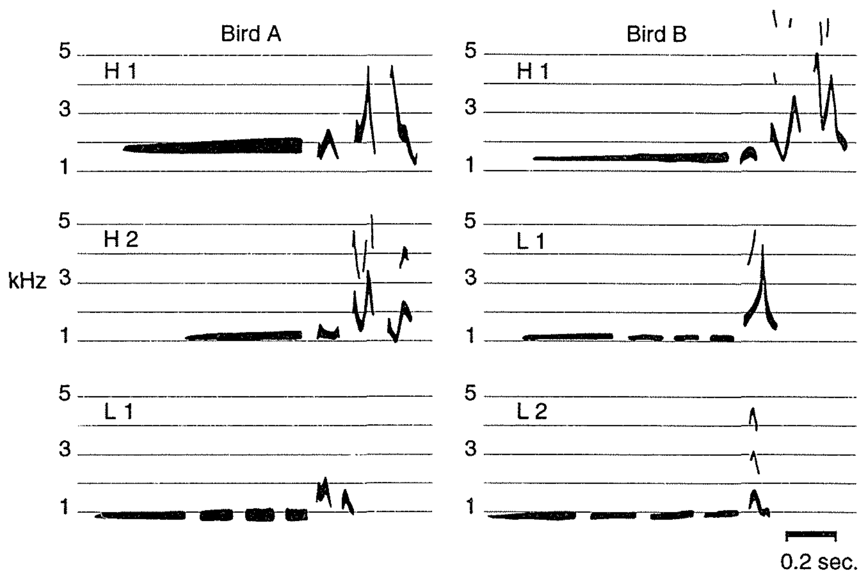

Fig. 1. Song repertoire of two wild male Bush Warblers. The bird A was recorded on 3 May, 1985 at Togakushi, Nagano, and the bird B was recorded on 28 April, 1982 at Hacchodaira, Kyoto.

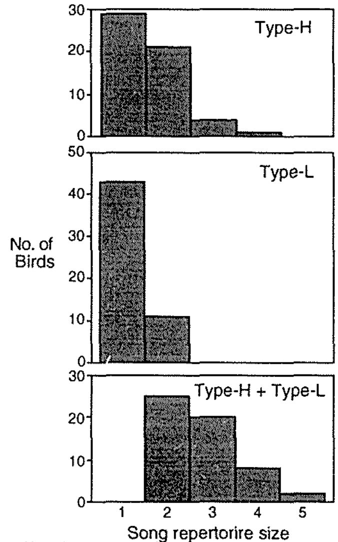

Fig. 2. Histogram showing the distribution of song repertoire size counted from 55 individually maked Japanese Bush Warblers.

Parameter	Explanation
CF_Freq	Frequency of the CF note(s)
FM_Len	Length (duration) of the FM part
FM_Min	Minimum frequency of the FM part
FM_Max	Maximum frequency of the FM part
FM_Range	Frequency range of the FM part
N_Note	The number of notes in a song
N_Infl	The number of frequency inflections

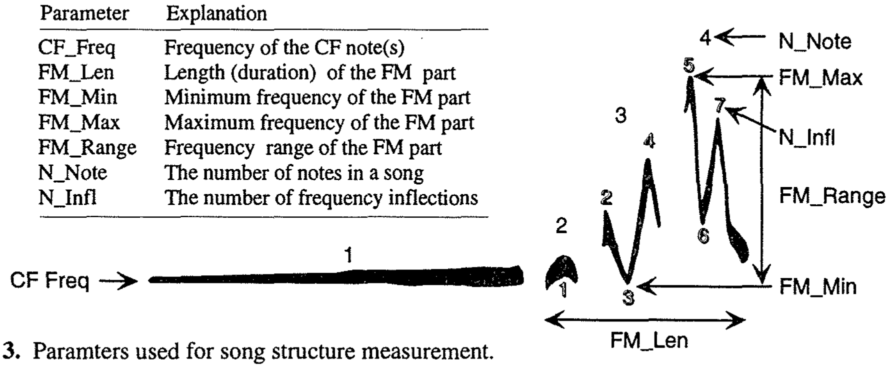

Fig. 3. Paramters used for song structure measurement.

quency) ($P = 0.169$). Table 2 shows the correlation matrix among these parameters. Again, all parameters showed high correlation values, while FM_Min showed lower correlation with others and tended to be rather constant (the coefficient of variation was 0.134 for type-H and 0.128 for type-L songs).

Fig. 4 shows the relationship between the CF frequency and the parameters related to FM structure. Among several parameters of FM structure, maximum FM frequency, FM frequency range and number of FM notes were positively related to CF frequency while minimum FM frequency tended to be constant over song types. Thus, there was a clear tendency that song types with higher CF frequency had higher FM frequency, wider frequency range and more complex structure. Fig. 5 shows the relation between the FM frequency range and the complexity of the song measured as the sum of the number of notes in a song and the number of frequency inflections in the FM part of the song. As shown in this figure, the song repertoire of the species forms a gradation of frequency range and complexity.

Table 1. Summary of structure measurement on the songs of the Japanese Bush Warbler. See Fig. 3 for the explanation of the measurement parameters. C. V. means the coefficient of variation (C. V. = S. D. / Average).

		CF_Freq	FM_Min	FM_Max	FM_Range	FM_Len	N_Note	N_Infl	Complex
Type-H	Average	1.515	1.136	4.251	3.116	.374	3.155	8.265	11.419
	S. D.	.321	.153	.819	.777	.079	.472	2.690	2.894
	C. V.	.212	.134	.193	.249	.211	.150	.325	.253
	N	155	155	155	155	155	155	155	155
	Min.	.877	.791	2.561	1.638	.183	2	3	5
	Max.	2.348	1.715	5.794	4.696	.597	5	16	21
Type-L	Average	.909	1.160	3.052	1.892	.187	1.991	4.144	6.135
	S. D.	.094	.149	.685	.647	.076	.640	2.088	2.542
	C. V.	.103	.128	.225	.342	.406	.321	.504	.414
	N	111	111	111	111	111	111	111	111
	Min.	.711	.798	1.549	.632	.053	1	0	2
	Max.	1.296	1.494	4.854	3.716	.397	3	11	14

Table 2. Correlation matrix among the structural parameters of the songs of the Japanese Bush Warbler. See Fig. 3 for the explanation of the parameters.

	CF_Freq	FM_Min	FM_Max	FM_Range	FM_Len	N_Note	N_Infl	Complex
CF_Freq	1.000	.181	.642	.629	.694	.612	.611	.642
FM_Min		1.000	.233	.078	-.058	-.157	-.031	-.059
FM_Max			1.000	.988	.694	.518	.665	.668
FM_Range				1.000	.721	.556	.687	.694
FM_Len					1.000	.879	.796	.853
NNote						1.000	.707	.804
NInfl							1.000	.989
Complex								1.000

Shifting of CF frequency

The CF frequency (the pitch of the CF part of the song) varied each time the bird uttered its song while FM part remained stable (Fig. 6). Fig. 7 shows the histograms of the CF frequencies of ten birds. In all birds, each song type had a fixed range of CF frequency shift, and the ranges showed little or no overlap among song types. Note that the naming of the song types such as H1, H2, L1, L2 is based on the relative pitches of corresponding CF notes.

Song type sequence

Song type sequence was analyzed in two captive birds and one wild bird. The results are shown in Fig. 8 as the matrix of transition probabilities (Bakeman & Gottman 1986). The probability of self-transition, the repetition of the same song (shown as circle-shaped arrows), was significantly lower than the transition to different patterns (cell by cell Chi-square test : $P<0.01$). Thus, the birds tended to avoid the repetition of the same song pattern and preferred alternation of different patterns.

Song interval

The time interval between two successive songs was measured in 4 birds. The results are shown in Fig. 9. The distribution patterns were nearly the same in all birds. There was no clear peak in the distribution and in recording songs in the field, it was always difficult to predict the precise timing of the onset of the next song.

Sound pressure level

The results of sound pressure level (SPL) measurement are shown in Fig.10. The SPL for the notes from type-L song were lower than type-H songs. Also, within a song type, SPL of FM notes were always lower than CF notes.

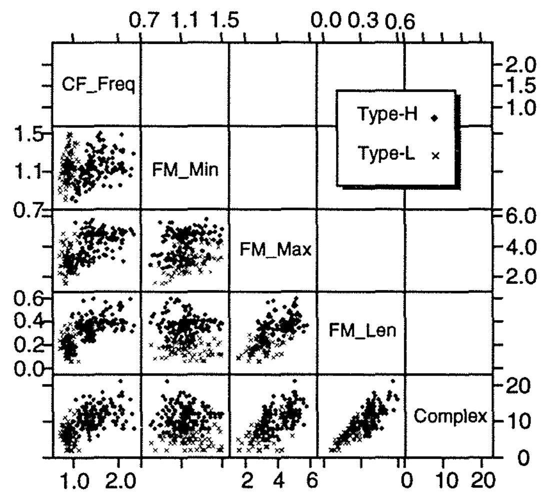

Fig. 4. Relationship between the CF frequency (CF_Freq) and several parameters related to the structure of the FM_part (FM_Min, FM_Max, FM_Len and Complex) of the Japanese Bush Warbler's song. See Fig. 3 for the explanation of each paramter.

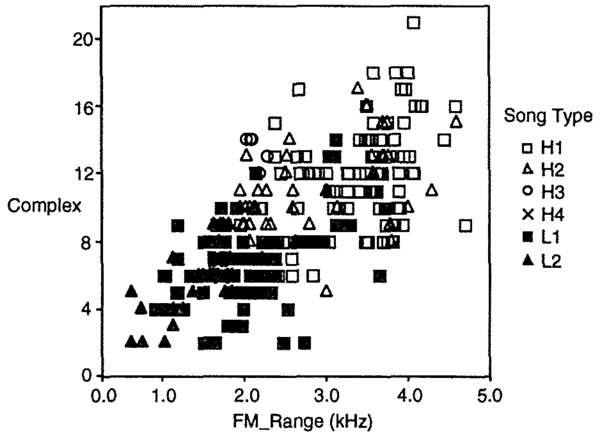

Fig. 5. Relationship berween the FM frequency range (FM_Range) and the complexity index (Complex) of the Japanese Bush Warbler song. See Fig. 3 for explanation of the parameters.

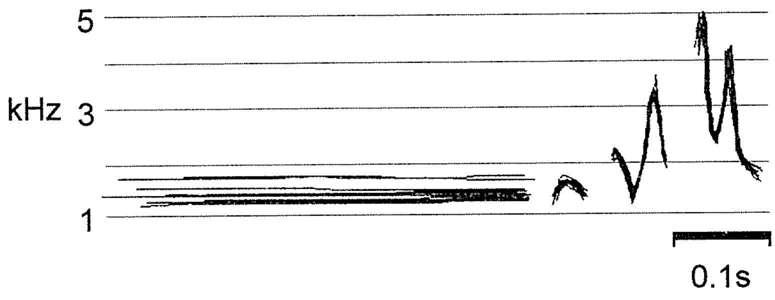

Fig. 6. Sonograms of 10 type-H songs sung by a male Japanese Bush Warbler, traced and imposed on each other.

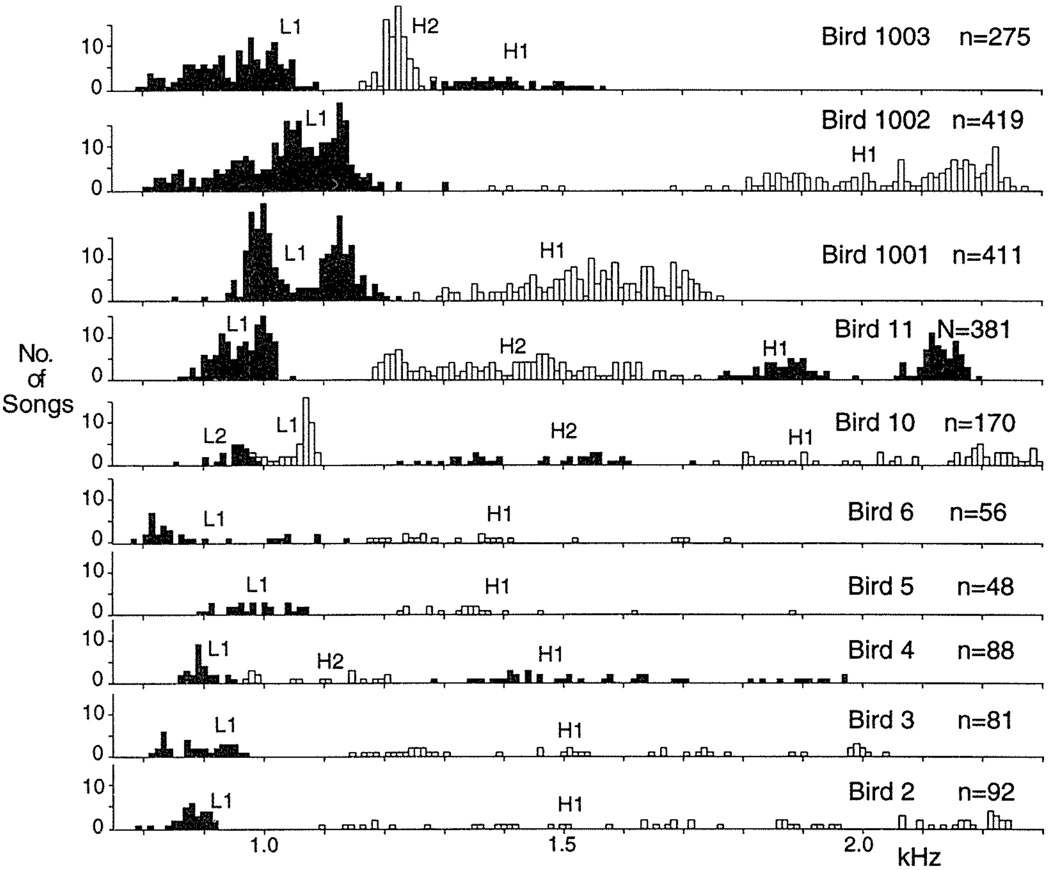

Fig. 7. Histograms showing variations and ranges of the CF frequency (pitch) of the 10 Japanese Bush Warblers' song. The data for 3 birds (Bird 1001-1003) were from laboratory recordings and data for 7 birds (Bird 2-11) were from field recordings.

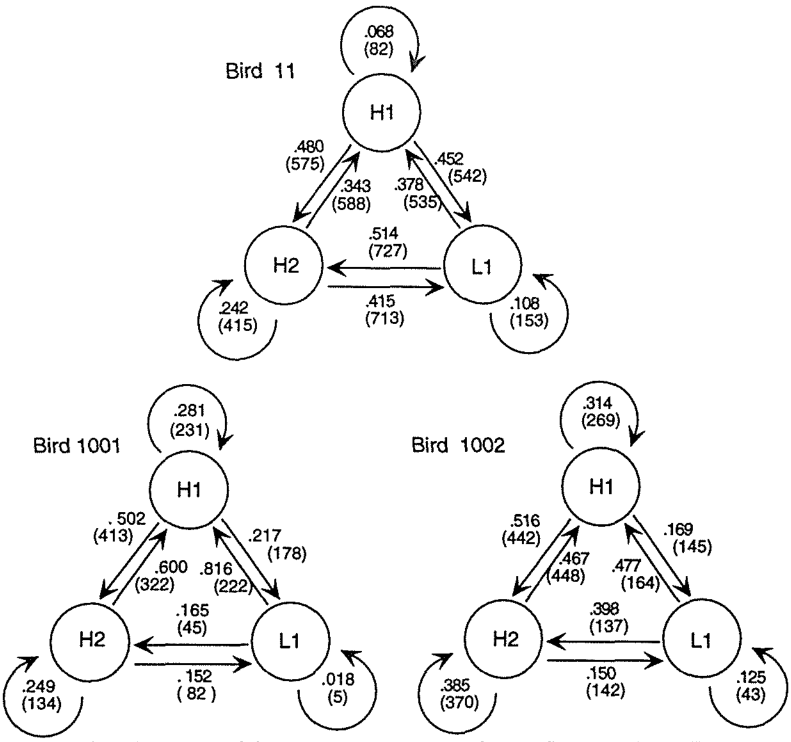

Fig. 8. State transition diagrams of the song type sequence from 3 Japanese Bush Warbler song recordings. The number beside each arrow shows the transitional probability for each song type transition. The number in the parentheses shows the actual transition frequency (number of cases observed).

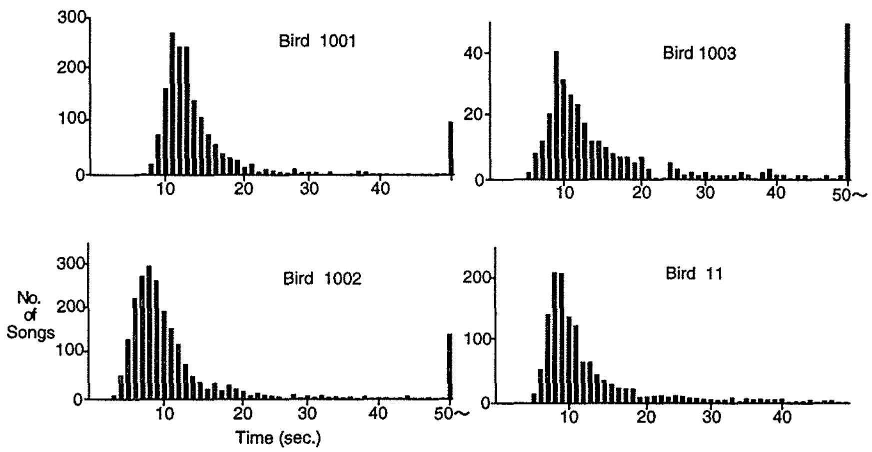

Fig. 9. Histograms showing the time intervals between two successive songs of the 4 Japanese Bush Warblers. The time interval was measured from the end of one song to the end of next song. The values that were longer than 50 sec. were totaled and shown as the rightmost column of each histogram. The data for bird 1001, 1002 and 1003 were from laboratory recordings and the data for bird 11 were from field recordings of a spontaneously singing wild bird.

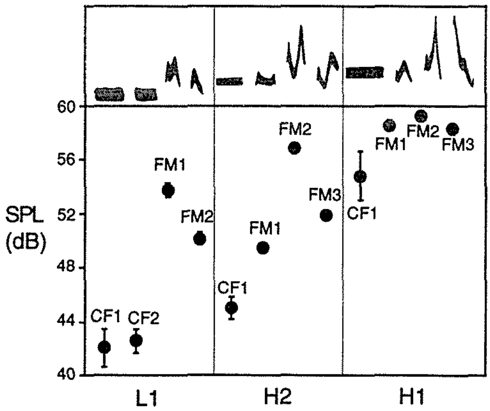

Fig. 10. Loundness (Sound Pressure Level) of a Japanese Bush Warbler's song. Each point shows the avarage ± s.d. of 10 songs of a same song type. The 4 points in each song type correspond to the measurements of the last 4 notes of the song. In case of type L1, the first 2 notes were from the CF part (CF1 and CF2) and the last 2 notes were from the FM part (FM1 and FM2).

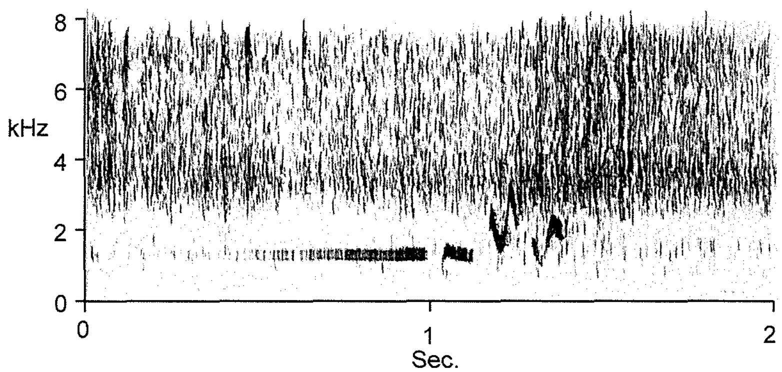

Fig. 11. An example of Japanese Bush Warbler's song (type-H) sung in the noisy (windy) environment.

Discussion

Songs of the Japanese Bush Warbler had several features, which could be the adaptations for long range communication in the bushy environment. The repertoire size was small (2-5), and songs were low-pitched (1.8 – 5.8 kHz in range) and were made of pure tones. Each song began with what could be considered as an alerting component (the CF part) followed by the FM pattern, which was very stable each time and thought to be the main body of the signal. The frequency range of the typical environmental noise of the species' habitat, which was mainly caused by bamboo leaves, was about 3 to 8 kHz (Fig. 11). The frequency range of the Bush Warbler's song was mostly lower than that (see background noise and a type-H song in the sonogram shown in Fig. 11).

However, the songs also had some features that were clearly not effective in the long range signal transmission. The bird changed the CF frequency each time, changed the time interval between songs, did not repeat the same pattern and preferred alternation, which also increased the variation in loudness, frequency range and the structural complexity of the song. As a result of this, the species' song is a rather unpredictable system in that a listener cannot foretell which pattern comes next and when, nor can it tune its hearing mechanism to an anticipated frequency.

The only explanation for these variable song parameters seems to be that they are anti-habituation mechanisms that reduce 'Monotony' of the songs (Hartshorne 1956). In many bird species, versatility of the song is attained by increasing repertoire size, and one possible function of the song repertoire is the reduction of habituation which would otherwise be formed by listeners, in this case 'floaters' that are seeking territories to invade in (Krebs 1976). The results of the playback experiment show that the response to the repetition of the single song type drops more sharply in time than the response to the variable, normal singing pattern of the species (Momose in prep. a). The song of the Japanese Bush Warbler is unusual in that the frequency of a component (CF frequency) is shifted while retaining the time-frequency structure of other components (FM part). This is another way of increasing song versatility without increasing repertoire size. The variable singing of the species might be an example to support anti-habituation hypothesis of Krebs (1976) from a different angle.

The problem that remained unanswered is why the species did not evolve a larger repertoire size. In view of the song repertoire size, there are two groups of birds; the versatile and continuous singers with large repertoire size and discontinuous singers which sing discrete, stereotyped songs with small repertoire size (Ince & Slater 1985). Catchpole (1982) argued that a bird species in which male-male competition is strong tends to have small repertoire sized songs mainly used for territorial defense. Bush warbler is a typical member of this group. One possible factor that might limit the repertoire size in this group of birds is the effectiveness of individual recognition between territorial neighbours. Individual recognition is clearly demonstrated in species with small repertoire size and even more clearly in species with a single song (Brooks & Falls 1975), but in species with larger song repertoire it is not so clearly demonstrated (Kroodsma 1976, Falls 1982). As the name indicates, Japanese Bush Warblers live in dense vegetation. In such an environment, the necessity for recognizing neighbours by songs must be strong since the birds cannot see one another. Indeed, the Bush Warblers recognize neighbours very clearly by their songs alone (Momose in prep. b). The structure of Bush Warbler's song could be understood as a compromise between two different contexts in male-male interaction: owner-floater context and owner-neighbour context. In the former context, song must sound complex but in the latter repertoire size must be small. Way of compromising in this species is an unusual one: the birds do not change the patterns of the signal but shift them in time and space. This unique style of singing behaviour might have evolved under the unique environment of the species' typical habitat, the dense bush.

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