

Does the Bush Warbler (*Cettia diphone*) Defend Its Territory through a Particular Song Mode or a Mode Sequence?

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The song of the bush warbler, *Cettia diphone*, consists of an introductory whistle portion and a complex ending syllable portion. In bush warblers, a song with two or fewer notes in the whistle portion is classified as an α song mode, while a song with three or more notes in the whistle portion as a β song mode. Although some variations occur in mode selection by individuals and populations, the proportion of α mode songs to total songs is 55% (range 51.6-58.7%) on average. The α mode has a higher dominant frequency in the whistle portion than does the β mode, but the number of syllables in the complex ending syllable portion is fewer. Bush warbler mode sequences are defined as $\alpha\alpha$, $\alpha\beta$, $\beta\alpha$, and $\beta\beta$ mode sequences. In order to test the hypothesis that song modes and mode sequences play a role in the defence of territory in Jeju and Wando populations in the south-coastal geographic song variation group, playback experiments were executed. Mode sequences differed between naturally produced songs and songs produced in response to playback for two populations. In particular, for birds in the Wando populations our results indicate that the use of song modes may be affected by habitat, singing site and type of territory, and further propose that particular mode sequences may play a more important role than song mode in vocal interactions.

KEY WORDS: Bush Warbler, Song Mode, Mode Sequence, Geographic Song Variation

Male song birds generally sing variable songs, and those variations are categorized into 'song types' (Kroodsma, 1982). The males of some species have distinctly different song types, such as the song forms (I, II) of the blue-winged warbler, *Vermivora pinus* (Kroodsma 1988), the repeat and serial modes of the American redstart, *Setophaga ruticilla* (Lemon *et al.*, 1987), and the repeat and mixed modes of the hooded warbler, *Wilsonia citrina* (Wiley *et al.*, 1994). Some studies have investigated the function of particular

song modes in different situations (Lein, 1978; Kroodsma, 1988; Wiley *et al.*, 1994). The study of the function of the two distinct song types of the blue-winged warbler according to geographic location showed that differing degrees of intra- and inter-sexual selection on two song forms may have promoted variation in one type and stereotyping in the other type (Kroodsma *et al.*, 1984).

Sequences of the song repertoire may be non-random, *e.s.* with repetition of all song types and alternation of some. Songs with similar sexual and aggressive messages are often associated in

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sequence (Smith, 1977; Payne, 1979; Falls, 1974). Smith (1991) suggests that a singer can keep abreast of significant changes by altering cadences and the ratios of different signal components, or reveal a steady state by maintaining one pattern.

The song of the bush warbler (*Cettia diphone*) consists of an introductory whistle portion and a complex ending syllable portion. Its repertoire is relatively small, so it can be assessed easily (mean = 1.94, N = 63 individual, range: 1-4). Bush warbler songs can be separated into two geographic variation groups; the Inland and the South-coastal groups, approximately divided by the 35° 35' N latitude (Yoon, 1995). In the Inland group, each song type is repeated several times before another is introduced (i.e., AAA...BBB...CCC...), while each song type in the South-coastal group often occurs every second or third song (i.e., ABABABCAB ...). Yoon (1995) suggests that song types may differ in note numbers in the whistle portion. In bush warblers, a

song with two or fewer notes in the whistle portion is classified as an α mode song and a song with three or more notes in the whistle portion as β mode song (Fig. 1). In the South-coastal group, each male uses its song modes in either of the following sequences: $\alpha\beta\alpha\beta\alpha\beta$ or $\alpha\beta\alpha\beta\alpha\alpha\beta$ (ie Fig. 1). We defined mode sequence pairs (Slaters, 1981), so for example in the latter sequence there was one $\alpha\alpha$ sequence, three $\alpha\beta$ sequences, two $\beta\alpha$ sequences, and one $\beta\beta$ sequence.

In the present study, we test the hypothesis that song modes and mode sequences play a role in the defence of territory. In order to test this hypothesis, playback experiments were executed in the south-coastal Wando and Jeju populations. Further the numerical characteristics of α and β modes of the three south-coastal populations, Wando, Geoje, and Jeju, were clarified.

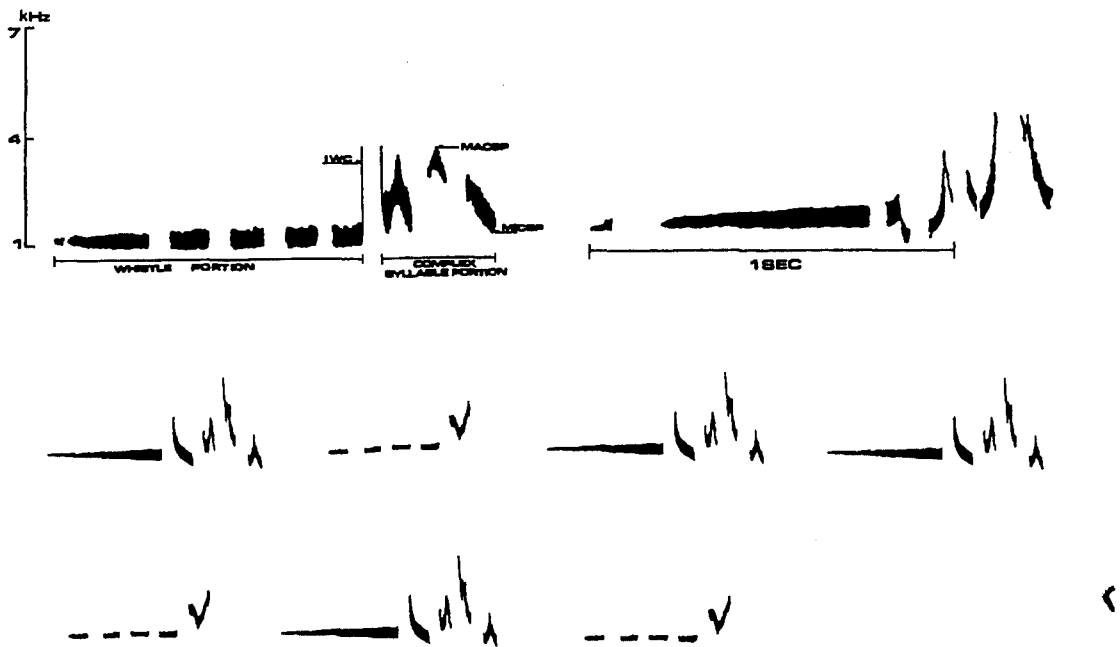


Fig. 1. The typical song modes and mode sequences of Bush warbler. The figure at the top shows two song modes; left, β song modes; right, α song mode. Lower figure shows partial sequence pairs ($\alpha\beta\alpha\beta\alpha\beta$) of bush warbler songs from Jeju population. mode sequence pairs are composed of one $\alpha\alpha$, three $\alpha\beta$, two $\beta\alpha$, and zero $\beta\beta$ sequences.

Materials and Methods

Song recordings for quantitative analysis of α and β modes

From April to July 1992 and 1993, the songs of 28 male bush warblers in the Jeju, Geoje, and Wando populations were tape-recorded and their songs analyzed. The number of songs and individuals involved in the recordings were as follows: 178 songs of 16 individuals from Jeju, 78 songs of six individuals from Geoje, and 63 songs of six individuals from Wando. Recordings were made at a tape speed of 19 cm per second using a Uher 4000 Report IC tape recorder, and with an AKG c1000s microphone mounted on a 54 cm parabolic reflector. The 319 songs of the 28 males were analyzed by a Kay Electric sonagraph, Model 5500, set for a wide band spectrum and eight song parameters (Fig. 1). The numbers of song types and syllables from each song were also measured from the sonagraph.

Study areas for the playback experiments

One area for the playback experiments was selected at Hado-Ri on Jeju island, nearly 200 km from the Korean peninsula. This study area is surrounded by a road. An average of 12 vehicles per hour, occasionally making loud noises, use the road. The location is approximately 0.5 km from the seashore, and includes a temple and an orchard. The dominant tree species in the 4 Km² area are *Robinia pseudo-acacia*, *Pinus densiflora*, *Quercus spp.*, *Rubus oldhamii*, *Rubus sorbifolius*, *Berchemiaefolia* and *Rubus schizostylus*.

The Wando study area is located about 1 km from the seashore. The area is dominated by two shrub-covered hills, which continue to bush areas

of 3-50 m width at the base. The study area consists of two sites separated by 150-200 m and about 50 farmhouses. Each bird's territory adjoins its neighbours' territories along a hill. There are sometimes two or three neighbouring territories at upper and lower locations. This means one territorial male has as many as three neighbours. There is a road about 200 m from the study sites, with an average of three vehicles per hour. The dominant trees are *Quercus denrata*, *Quercus aliena*, *Camellia japonica*, *Picea jezoensis*, *Rubus crataegifolius* and *Phaseolus thunbergiana*.

Playback experiments

Each six male from Jeju and Wando was subjected to playback recordings of natural songs, α song modes only, and β song modes only (Fig. 1). Two songs of each mode were prepared from Geoje and Chiba (in Japan) populations, and natural songs were recorded from Jeju which is some distance from our study population. Each stimulus song was played for 3 minutes. Two modes were recorded on a cassette tape with one song every 10 seconds. Natural stimulus song was not manipulated in their proportion of song modes and mode sequences, so it had natural song intervals and mode sequences (about 10 s.) (Table 1).

Territorial boundaries were observed and predetermined before the field tests. The normal songs of 12 males were recorded for comparison with the songs in response to playback stimulus tests. Each stimulus song was played by using a three-headed cassette-recorder (Sony TCM-5000EV) always at the centre of the bird's territory. The volume of the playback stimulus songs was adjusted to 90 dB at 1 m from the

Table 1. Mode sequences of stimulus songs, α and β song modes, and naturally-produced songs.

Stimulus songs	Mode sequences
Natural	$\alpha^1 \beta^1 \alpha^2 \alpha^3 \beta^2 \alpha^4 \beta^3 \dots \alpha^8 \beta^7 \alpha^9 \alpha^{10} \beta^8 \alpha^{11}$
α mode only	$\alpha^1 \alpha^2 \alpha^3 \alpha^4 \alpha^5 \alpha^6 \dots \alpha^{16} \alpha^{17} \alpha^{18}$
β mode only	$\beta^1 \beta^2 \beta^3 \beta^4 \beta^5 \beta^6 \dots \beta^{16} \beta^{17} \beta^{18}$

The number indicates each song mode time represented during playback.

speaker using a precision integrating sound level meter (Larson Davis Laboratories Model 800B). A standard set of stimulus songs was presented in random order to each territorial male. Nearly all experiments were carried out between 6:30-11:00 a.m. from 3 to 9 April 1995 at Jeju, and from 10 to 12 May 1995 at Wando. Each playback commenced only when the bird was singing. In all cases, the songs in response to each stimulus song during playback were recorded in the same way as the normal songs to enable a comparison.

Analysis

The naturally-produced normal songs of the 12 subjects were analyzed by a Kay Electric sonagraph, Model 5500, set for a wide band spectrum. The recorded normal songs consisted of 336 from Jeju and 333 from Wando. The normal songs were analyzed to count the proportion of song modes from each male and to test for any shifts in mode sequences.

The response songs of the 12 subjects were 279 from Jeju and 232 from Wando, and were analyzed in the same way as for the naturally-produced songs. The degree of song matching during the playback was also calculated. 241 mode sequences from Jeju and 226 from Wando were analyzed and classified on the basis of Slater's study (1981). In cases in which one mode has two song types, the two types were classified into the same mode as in Slater (1983).

The numerical characteristics of the two modes at Jeju, Wando and Geoje, and differences between normal songs of the Jeju and Wando populations were analyzed by a mean test, correlation analysis, one-way ANOVA and the Wilcoxon matched-pairs signed-ranks test. For the comparison of normal songs and response songs recorded during playback to analyse shifts in the mode sequence and the proportion of each song mode, Chi-square tests were used exclusively.

Results

The quantitative characteristics of song modes, α and β

Figure 1 shows the representative α and β

modes of bush warbler songs from the Geoje area. The results of song mode selection in relation to studied populations are as following: two out of the 16 Jeju individuals sang only the β mode in Jeju, while all other individuals sang the α and β modes. The proportion of α mode to analyzed entire songs are as follows: 58.7% in Wando, 53.8% in Geoje and 51.6% in Jeju. Within an α mode, song duration (SD) and the duration of the whistle portion (DWP) shows a positive correlation ($r = 0.7385$, $n = 24$, $p < 0.001$), as does SD and the duration of complex syllable portion (DCSP) ($r = 0.5507$, $n = 24$, $p < 0.001$) show a positive correlation, whereas SD and the minimum frequency of complex syllable portion (MICSP) ($r = -0.5517$, $n = 24$, $p < 0.001$) show a negative correlation. Within a β mode, only correlation between SD and DCSP ($r = 0.7380$, $n = 25$, $p < 0.001$) is significant.

In an analysis of eight song parameters (Table 2), the dominant frequency of the whistle portion (DFWP) and the maximum frequency of the complex syllable portion (MACSP) of the α mode are higher than those of the β mode. Also, the SD and the DCSP of the α mode songs are longer than those of the β mode songs in all recorded populations (Table 2). Song parameters show significant differences between α and β modes in all localities. The differences are: the number of notes in whistle portion (NNWP), DFWP, the interval between the whistle portion and the complex syllable portion (IWC), SD, DCSP ($df = 1, 21$, $P < 0.05$) for Jeju, NNWP, DFWP, DWPMICSP, SD, DCSP ($df = 1, 12$, $p < 0.05$) for Geoje, and NNWP, DFWP, IWC ($df = 1, 10$, $p < 0.05$) for Wando population.

Twenty eight males have 58 (2.1 ± 0.66 , $n = 28$) song types, and one individual has song types ranging from one to four. Each mode has as many as 29 song types. The number of individuals by the number of song types categorized is as follows: 2 individuals have only one song type, 20 individuals have two song types across all populations, 5 individuals have three song types, and 1 individual has four song types. The α mode has a range of syllables from two to five (3.61 ± 0.66 , $n = 134$), and the β mode has a range of syllables from one to four (2.31 ± 0.89 , n

Table 2. The characteristics of α and β modes on the eight song parameters of bush warbler at Jeju, Geojedo, and Wando populations.

Parameters	Jeju (df=1,21)		Geojedo (df=1,12)		Wando (df=1,10)		Total (df=1,45)	
	α	β	α	β	α	β	α	β
Whistle portion	1.42±0.40*	4.41±0.63*	1.31±0.45	4.29±0.35*	1.27±0.39	4.46±0.45*	1.38±0.34	4.45±0.61*
Number of notes								
Dominant	1607.45	950.13	1530.28	917.41	1592.60	961.53	1591.09	945.16
Frequency (Hz)	±105.21	±32.43*	±247.35	±61.93*	±294.57	±60.72*	±152.25	±30.56*
Duration (sec)	0.78±0.17	0.68±0.13	0.92±0.22	0.75±0.15*	0.66±0.25	0.71±0.24	0.82±0.20	0.72±0.12*
Interval between Whistle and Complex portion (sec)	0.05±0.00	0.04±0.00*	0.04±0.00	0.04±0.00	0.05±0.00	0.04±0.00*	0.05±0.00	0.04±0.00*
Complex syllable								
Maximum	4705.42	4117.66	4948.57	3468.75	4283.84	3396.92	4629.54	3755.19*
Frequency (Hz)	±487.55	±832.05	±360.02	±504.06*	±456.04	±78.42	±574.45	±731.54
Minimum	1103.76	1034.38	1022.85	1035.00	970.51	1143.07	1065.99	1047.45
Frequency (Hz)	±142.75	±122.14	±124.99	±64.38	±73.66	±66.11	±157.60	±141.17
Duration (sec)	0.40±0.16	0.27±0.06*	0.39±0.06	0.10±0.02*	1.22±0.23	1.00±0.22	0.38±0.11	0.22±0.10*
Song Duration (sec)	1.32±0.25	1.01±0.16*	1.39±0.17	0.86±0.27*	1.22±0.23	1.00±0.22	1.32±0.21	0.98±0.16

*: Significant, $P < 0.05$ (One-way ANOVA between α and β modes' parameters) +; Standard deviation (S.D.)

= 134) in a song, but the difference between the two modes is not significant ($p < 0.808$). The correlation between NNWP and the number of syllables is significant ($r = -0.5860$, $P < 0.001$).

Playback experiments

Table 3 shows the proportion of song modes and mode sequences in naturally-produced songs from two study populations. The proportion of song modes between the two populations is not

Table 3. The differences of the proportion of song modes and mode sequences on naturally produced songs from Jeju and Wando.

Populations	Articles	Song Modes (%)		Mode Sequence (%)			
		α	β	$\alpha\alpha$	$\alpha\beta^*$	$\beta\alpha^*$	$\beta\beta^*$
Jeju (N=6)		51.27	48.73	24.06	31.81	31.60	9.82
Wando (N=6)		52.28	47.72	33.24	19.64	17.65	38.08

*; Differences between Jeju and Wando to each mode sequence are significant, $P < 0.05$ (One-way ANOVA)

Table 4. Comparison of the proportion of α mode between naturally produced song and song responded during playback at Jeju and Wando.

Stimulus songs	α song mode			
	Jeju (df.=24, 279 songs)		Wando (df.=22, 232 songs)	
	Observed	Expected	Observed	Expected
Natural	19	19.63	12	28.08
α mode only	87	58.09	16	68.14
β mode only	89	65.87	15	45.48
Total	195	143.59	43	141.7
χ^2	18.41		68.75**	

** $P < 0.001$ (Chi-square test). The expected is calculated as follows: Expected = $(A \times B)/100$. A = the number of total responded songs during playback experiments, B = the percentage of α mode in naturally produced songs.

Table 5. Comparison of the proportion of mode sequences between naturally produced songs and songs responded during playback at Jeju.

Stimulus songs	Mode sequences (df.=24, 241 sequences)							
	$\alpha\alpha$		$\alpha\beta$		$\beta\alpha$		$\beta\beta$	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
natural	5	7.74	12	10.76	12	11.00	5	2.49
α mode only	49	22.05	17	29.76	18	30.61	9	10.03
β mode only	50	26.88	30	37.36	31	36.10	3	12.83
Total	104	56.67	59	77.88	61	77.71	17	25.35
χ^2	39.20*		4.58		3.59		2.75	

* $P < 0.05$ (Chi-square test). The expected is calculated as follows: Expected = $(A \times B)/100$.

A = the number of total responded mode sequences, B = the percentage of each mode sequence in naturally produced songs.

Table 6. Comparison of the proportion of mode sequences between naturally produced song and songs responded during playback at Wando.

Stimulus songs	Mode sequence (df.=22, 226 sequences)							
	$\alpha\alpha$		$\alpha\beta$		$\beta\alpha$		$\beta\beta$	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
natural	6	14.49	5	10.52	5	9.21	30	11.05
α mode only	6	41.06	14	27.72	13	22.75	75	22.12
β mode only	5	26.29	9	16.17	10	14.33	48	15.83
Total	17	81.84	28	54.41	28	46.29	153	49.00
χ^2	51.37**		12.82		7.23		220.73**	

** : P<0.001 (Chi-square test)

significant (α : df = 1,9, F = 0.0175, P = 0.8977; β : df = 1,9, F = 0.0177, P = 0.8970). The proportion of mode sequences is significant as follows: $\alpha\beta$ (df = 1,9, F = 9.5891, P<0.05), $\beta\alpha$ (df = 1,9, F = 21.2899, P<0.01), and $\beta\beta$ (df = 1,9, F = 5.3955, P<0.05); but the difference of $\alpha\alpha$ sequence is not significant (df = 1,9, F = 1.4375, P = 0.2612). The differences between $\alpha\alpha$ and $\beta\alpha$ mode sequences within each population are significant in the two populations (Wilcoxon matched-pairs signed-ranks test, Wando: z = -1.9917, p<0.05; Jeju: z = -1.9917, P<0.05).

Ten subject males responded to playback with one song type per mode, while two males responded with two song types in one of each of the α and β modes. All males show song matching to stimulus songs. The percentage of positive song matching to the α mode is 72.36%, and to the β mode is 60.42%. The proportion of α mode songs sung during playback experiments significantly decreases in the Wando population (df = 24, Chi-square = 68.75, P<0.001), but at Jeju, it is not significant (Table 4). In the Jeju population, the proportion of mode sequences during playback experiments is significant in the $\alpha\alpha$ sequence (df = 24, Chi-square = 39.20, 0.02<P<0.05) (Table 5); and in Wando, the proportion of the $\alpha\alpha$ (df = 22, Chi-square = 51.37, P<0.001) and the $\beta\beta$ (df = 22, Chi-square = 220.73, P<0.001) sequences are significant (Table 6).

Discussion

In this paper, we examine birds' production of particular song modes (Cowlshaw, 1992) and mode sequences (Smith, 1991) for territory defence in bush warblers of the south-coastal geographic populations.

Considering that the α mode has a higher dominant frequency within the whistle portion than that of the β mode, the α mode could mainly be used for nearby listeners (Smith, 1991; Nowicki *et al.*, 1994), while the β mode could chiefly be used for the distant listeners. Lemon *et al.* (1987) proposed that the differences in acoustic qualities of the different songs of warblers may be important for the reason of distance. Our normal songs did not show the different proportion of the two song modes; and at Jeju the differences of the song mode proportion during playback was not significant. This result suggests that, although bush warblers ordinarily might transmit a message to listeners at both far and near distance (Falls, 1969; Richards, 1981), in less stable circumstances where an intruder sings to start contests or a newcomer may sing to elicit information by probing (Smith, 1991), the two modes might commonly play a role in territory defence. But the question still remains as to why birds need to transmit messages to distant as well as near listeners in the South-coastal group.

In the study of repertoire sequences, it is important that the complex song sequences of birds are understood as simple sequences according to their characteristics (i.e., first order)

(Slater, 1983). Bush warbler songs are divided into two modes by the characteristics of introductory notes (Yoon, 1995). So, the mode sequences of bush warblers can be divided simply into four categories: $\alpha\alpha$, $\alpha\beta$, $\beta\alpha$, and $\beta\beta$ sequences. The particular sequences of song presentation may determine how interactions between different individuals are achieved (Lemon *et al.*, 1993). Individuals may interact with each other at longer distances by selecting identical song types from their repertoires (Lemon, 1968; Horn and Falls, 1988). Between the two study populations, normal songs significantly show the different proportion in mode sequences, and Wando birds particularly have more $\beta\beta$ sequences than those of Jeju birds. During playbacks, our birds showed significant differences in the proportion of mode sequences between normal and responded songs. This result suggests that particular repetitive mode sequences act as an important factor for intra-competition like territory defence.

The differences between the Jeju and Wando populations in the proportion of song modes and mode sequences sung during playback may be caused by the different habitats, singing sites, and structure of territories. The distortion of sound in vegetated environments could divide into sound attenuation and degradation (Wiley and Richards, 1982). Particularly, for maximum efficiency, long-range acoustic communication in any habitat should employ the lowest frequencies possible because the lower frequencies attenuate less in all habitats (Wiley and Richards, 1982). Considering that the Jeju sites were open habitats composed mostly of bush areas, whereas the Wando sites were mostly deciduous habitats, sounds were scattered in the former area by atmospheric turbulence, and in the latter area by vegetation. So, individual songs of the Wando population could possibly be distorted more than that of the Jeju population. This limitation in the sound transmission forces individuals to select the lower frequency mode sequence ($\beta\beta$ sequences) instead of $\alpha\alpha$ sequences as in normal songs. This trend could also explain our results at Wando where individuals during playbacks responded with more β mode and more $\beta\beta$ sequences than those of the proportion of normal songs.

Studies on the differences in song sites and different territorial conditions occupied by separate populations can be proposed for a further interpretation on the different song selection mechanisms (Date, 1987). The subject males at Jeju generally sang on shrubs that rose independently high above the bushes. They often stopped their songs when they flew into the bushes. Whereas males at Wando usually sang within shrubby vegetation, although there were bushes in some places. This behavioural difference indicates that individual song transmission at Jeju is affected mainly by air conditions, whereas it is affected by air conditions and vegetation at Wando.

At Wando, we found that territorial males showed frequent song matching with nearby neighbours and with individuals of the opposite mounds; while at Jeju, song matching only occurred with neighbours of directly adjoined territories. Lemon *et al.* (1987) showed through detailed observations over one to three hours that birds' uses of particular modes correlated with exposure to a neighbour singing of the same mode. Particularly when a territory is not located on the same plane structure but on a different spatial structure, the use and function of repertoires and song modes in relation to habitat conditions must be considered in more detail.

In conclusion, our results demonstrate that individuals of Wando have been positively enforced to select a $\beta\beta$ sequence, while those of Jeju use an $\alpha\alpha$ sequence according to circumstances like habitats and threatening situations (Nowicki, 1994). Although song modes and mode sequences vary according to local populations, particular mode sequences play a more important role than do particular song modes for territory defence in the South-coastal geographic song variation group of bush warblers.

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털새권 방어와 관련된 휘파람새의 Song Mode와 Mode Sequence의 이용
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한국산 휘파람새(*Cettia diphone*)의 song은 도입부인 whistle부와 종결부인 syllable의 두 부분으로 구성되며, 그들의 song은 도입부에 나타나는 note의 수에 따라서 2개 이하의 것은 α song mode로 3개 이상으로 구성되어지는 song은 β song mode로 분류된다. 개체와 지역에 따라서 차이는 있지만 한 개체가 부르는 전체 song에서 α mode가 차지하는 비율은 약 55%(51.6~58.7%)이었다. α mode는 β mode에 비하여 whistle 부분의 dominant frequency는 높은 반면, syllable 부분을 구성하는 syllable들의 수는 상대적으로 적었다. 휘파람새의 mode sequence는 그들의 출현 순서에 따라서 $\alpha\alpha$, $\alpha\beta$, $\beta\alpha$, $\beta\beta$ 의 네 가지로 정의되었다. 휘파람새의 지리적 변이 그룹인 south-coastal 그룹 내의 개체군집인 완도와 제주에 있어서 song mode와 mode sequence는 그들의 털새권의 방어를 위하여 역할을 수행할 수 있다는 가설을 세우고 이를 검증하기 위하여 playback 실험을 수행하였다. 실험의 결과 mode sequence는 실험 전 자연 상태에서 녹음되었던 song과 playback의 실험 중에 녹음되었던 song과는 실험이 실시된 두 지역 모두에 있어서 의미 있는 차이를 나타내었다. 특히, 완도의 군집에서의 결과는 song mode의 사용이 서식지, singing site, 털새권의 공간적인 형태에 따라 영향을 받는다는 것을 나타낸다. 나아가 song을 통한 털새권의 방어에 있어서 특정의 mode sequence는 song mode 자체보다 더 중요한 역할을 할 수도 있을 것으로 생각된다.