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Song Structure and Microgeographic Variation in a Population of the Grey-cheeked Fulvetta (*Alcippe morrisonia*) at Shoushan Nature Park, Southern Taiwan

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Bao-Sen Shieh (2004) Song structure and microgeographic variation in a population of the Grey-cheeked Fulvetta (*Alcippe morrisonia*) at Shoushan Nature Park, southern Taiwan. *Zoological Studies* **43**(1): 132-141. This study examined the sonogram structure and microgeographic variation of songs of the Grey-cheeked Fulvetta (*Alcippe morrisonia*) at Shoushan Nature Park, southern Taiwan during March-July 2001. A typical song of the Grey-cheeked Fulvetta contained 2 distinct phrases, the 1st a whistled phrase and the 2nd a harmonic one. All recorded songs contained the whistled phrase, whereas some songs contained no harmonic phrase. Furthermore, within a bird sample (recorded from the same location), the number of syllables was consistent, whereas the number of syllables in the harmonic phrase was variable. Thus, song types, which were used for analyzing microgeographic patterns, were classified based on the whistled phrase without considering the harmonic phrase. The results of cluster analysis of song types revealed 2 song themes in this population: northern and southern. Major discrete boundaries could be illustrated based on these 2 themes, representing 2 major dialects. Furthermore, the northern theme group was subdivided by a minor boundary, and 2 small clusters of neighboring birds constituted subdialectal nuclei in which bird samples demonstrated the same song types. In the study population, dispersal across a control line between the 2 major dialects was unrestricted, but there was a dialect boundary in the absence of a geographic barrier in the study area.
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Key words: Song structure, Grey-cheeked Fulvetta, Syllable, Song type.

Geographic variation in songs is common and taxonomically widespread among birds and can be distinguished into 2 forms: macrogeographic and microgeographic (Mundinger 1982). Macrogeographic variation refers to differences that are found between populations, individuals from which are unlikely to meet each other. Significant marcogeographic differences between populations have been demonstrated in several species, such as Lincoln's Sparrows (*Melospiza lincolnii*) (Cicero and Benowitz-Fredericks 2000), Song Sparrows (*M. melodia*) (Peters et al. 2000), Willow Flycatchers (*Empidonax traillii*) (Sedgwick 2001), and Golden Bowerbirds (*Prionodura newtonia*) (Westcott and Kroon 2002). In contrast, microgeographic variation refers to song variations at a local level between neighboring birds that interact with each other within a population (Mundinger 1982, Nelson 1998). A dialect pattern is a particular form of microgeographic variation characterized by discrete boundaries between song forms (Mundinger 1982). Many causal models concerning the evolution of dialect patterns have been proposed, and describing microgeographic variation in song is fundamental to the direct testing of those different models (Catchpole and Slater 1995).

Syllables are the basic units of a song, and geographic variation in bird songs should be examined at both the whole-song level and the syllable level (Tracy and Baker 1999). Researchers have used syllable types to demonstrate dialect patterns in various species (Mundinger 1982). For example, based on syllable types and gargle types (a combination of syllables), dialects could be demonstrated in a Black-capped Chickadee (*Parus atricapillus*) population (Ficken and Weise 1984, Miyasato and Baker 1999). In the most widely studied species with regard to song dialects, the White-crowned Sparrow (*Zonotrichia leucophrys*), different dialects are distinguished based on differences in certain types of syllables in the terminal trills of songs (Baptista 1977, DeWolfe and Baptista 1995, Chilton and Lein 1996, Nelson 1998).

The Grey-cheeked Fulvetta (*Alcippe morrisonia morrisoniana*) is a sedentary endemic subspecies commonly found in lowland forests of Taiwan (Yen 1990, Chou et al. 1998, Yo 1999). In the non-breeding season, the Grey-cheeked Fulvetta leads foraging mixed-species flocks and often gives alarm calls in response to predators (Chen and Hsieh 2002). The Grey-cheeked Fulvetta breeds from Mar. to Aug., and sings throughout the breeding season from Feb. to Oct. (Lin 1996). It is monogamous without sexual dimorphism, and both sexes participate in parental care (Lin 1996, Kuo 2000). MacKinnon and Phillipps (2000) described the song of the Grey-cheeked Fulvetta as a sweet whistling, ji-ju ji-ju, usually followed by an undulating drawn-out squeaking element. Little is known concerning the structure or microgeographic variation of the songs of this species. Thus, the main objectives of this study were (1) to make a detailed description of its song structure using spectrographic analyses, and (2) to objectively evaluate microgeographic variation in the song pattern using both syllables and song types.

MATERIALS AND METHODS

Recording methods

I recorded the songs of the Grey-cheeked Fulvetta during Mar.-July 2001 at Shoushan Nature Park, previously called Chaishan Nature

Table 1. Sequence of whistled syllables and the number of harmonic syllables in songs recorded from 21 bird samples of the Grey-cheeked Fulvetta at Shoushan Nature Park

[a]Bird sample ID	No. of songs recorded	Whistled syllable sequence	Theme	No. of harmonic syllables in the song	Duration mean ± SE		
					Song	Whistled phrase	Harmonic phrase
N4	18	1 -2 -3 -4	Northern, main	1-3	1.264 ± 0.051	0.98 ± 0.009	0.243 ± 0.044
N5	7	1 -2 -3 -4	Northern, main	1-2	1.431 ± 0.072	1.032 ± 0.017	0.363 ± 0.066
N6	9	1 -2 -3 -4	Northern, main	2	1.813 ± 0.024	1.101 ± 0.019	0.683 ± 0.011
N8.1	19	1 -2 -3 -4	Northern, main	0-2	1.156 ± 0.036	1.064 ± 0.006	0.081 ± 0.032
N10	4	1 -2 -3 -4	Northern, main	1-2	1.469 ± 0.127	0.978 ± 0.019	0.450 ± 0.124
N21	23	1 -2 -3 -4	Northern, main	1-2	1.745 ± 0.018	1.080 ± 0.003	0.646 ± 0.018
N23	4	1 -2 -3 -4	Northern, main	1-2	1.639 ± 0.133	1.018 ± 0.052	0.588 ± 0.082
N9	9	1 -2 -3 -4b	Northern	2-3	1.731 ± 0.047	1.026 ± 0.031	0.672 ± 0.051
N7	5	1 -2 -3 -4c/d	Northern	1-3	1.962 ± 0.168	1.185 ± 0.028	0.698 ± 0.191
N8.2	9	1 -2 -3 -4e	Northern	1-4	1.904 ± 0.108	1.023 ± 0.028	0.865 ± 0.112
N25	4	1-1 -2 -3 -4	Northern	1-2	1.598 ± 0.075	1.201 ± 0.015	0.370 ± 0.086
N1	2	1 -2 -3a-4b	Northern	2-3	1.715 ± 0.2	0.811 ± 0.002	0.885 ± 0.201
N8.3	7	2 -3 -4	Northern	1-4	1.490 ± 0.237	0.794 ± 0.006	0.682 ± 0.240
N11	7	1a-2a-3-4	Northern	0-1	1.187 ± 0.057	1.101 ± 0.007	0.071 ± 0.046
N12	9	1a-2a-3-4	Northern	1-3	1.533 ± 0.074	1.060 ± 0.006	0.460 ± 0.074
N14	24	1a-2a-3-4	Northern	0-1	1.246 ± 0.016	1.047 ± 0.005	0.180 ± 0.014
S4	28	1 -2 -4a-3	Southern	0-2	1.677 ± 0.032	1.164 ± 0.008	0.491 ± 0.032
S6	10	1 -2 -4 -3	Southern	2-3	1.738 ± 0.055	1.013 ± 0.012	0.712 ± 0.053
S7	4	1a-2 -4-3	Southern	1-2	1.381 ± 0.055	0.939 ± 0.072	0.404 ± 0.103
N15	4	1-1a-3c-3d-5	N15	0-2	1.610 ± 0.017	1.610 ± 0.017	All unclear
N3	6	4b/c-3b-2	N3	2	1.832 ± 0.086	1.192 ± 0.029	0.612 ± 0.064

Sequences that are identical to the main theme (1-2-3-4) are shaded. Bird samples are arranged according to the results of cluster analysis.

[a]N8.1, N8.2, and N8.3 were counter-singing individuals at the same location.

Park, of Kaohsiung City in southern Taiwan (Fig. 1). The study area covers about 1000 ha, at an elevation of 356 m at its highest point. The vegetation of the study area is characterized as evergreen rain forest. Songs were recorded in the field using a Sony TC-D5 ProII recorder equipped with a Sennheiser ME67 unidirectional microphone. All recordings were obtained between 07:00 and 10:00 in the morning. I recorded an individual's songs until it either stopped singing or flew out of recording range. After each individual was recorded, its location was noted on a map (Fig. 1). Because the birds were not individually marked, songs recorded from different locations were considered to represent different bird samples when analyzing the microgeographic pattern of songs. In cases where I recorded songs at the same location on more than 1 d and the spectrograms were identical, those songs were classified as belonging to the same bird sample. All songs recorded from the same location were considered a single bird sample except for songs from counter-singing individuals at the same location which could be distinguished and therefore, considered to belong to different bird samples. Thus, 21 bird samples were recorded in this study (Table 1).

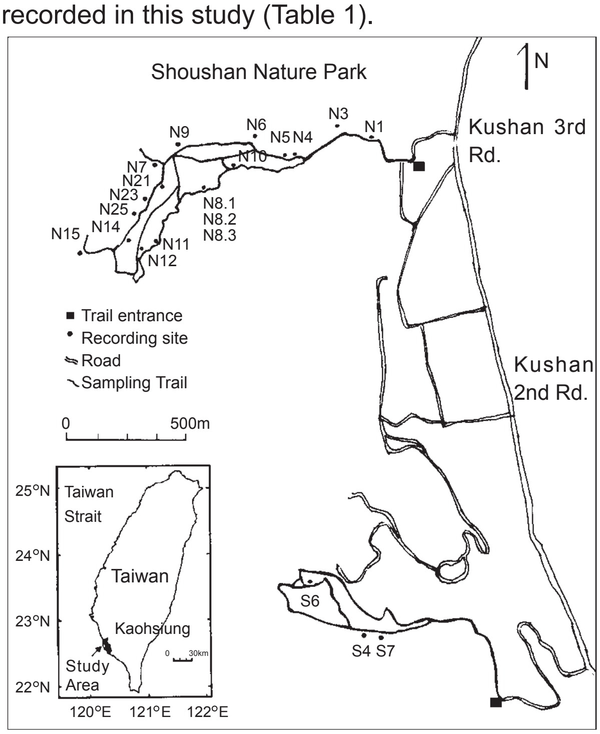

Fig. 1. Map of Shoushan Nature Park showing the locations where song recordings of the Grey-cheeked Fulvetta were made. Capital letters with numbers identify the bird samples at recording locations. N8.1, N8.2, and N8.3 were counter-singing individuals at the same location.

Measurements of acoustic structure

Songs were digitized and analyzed using Avisoft-SAS Lab Pro software (Raimund Specht, Berlin, Germany; with a sampling rate of 22.05 kHz, sample size of 8 bits, and FFT-length of 512 points). Sonograms were produced at 43 Hz of frequency resolution and 2.9 ms of temporal resolution. I defined phrases, syllables, and notes as suggested in previous studies (Mundinger 1975, Thompson et al. 1994, Miyasato and Baker 1999, Tracy and Baker 1999). A given syllable was separated from adjacent syllables by a silent period of 0.02 to 0.2 s and consisted of 1 or more individual notes. A note was a continuous tracing on a sonogram; it either overlapped in time or was separated from other tracings by less than 0.02 s.

Using the automatic parameter measurements option of the Avisoft-SAS Lab Pro software, the following variables were measured: duration of a song, duration of a phrase, duration of a syllable, peak frequency (the frequency of the maximum amplitude of the spectrum) at the start of a syllable, peak frequency at the end of a syllable, mean frequency of an entire syllable (derived from the average peak frequency of the entire syllable), minimum frequency of an entire syllable, and maximum frequency of an entire syllable.

Determination of syllable types and song types

According to the sonogram structures, a typical song was broken down into 2 phrases: whistled and harmonic (Fig. 2a). A whistled phrase had 3-5 syllables with whistled structures; a harmonic phrase had 1-4 syllables with harmonic structures.

I compared whistled syllables from each bird sample's repertoire with those from every other bird sample, and grouped like syllables from different bird samples together with consideration of syllable shape, duration, frequency, and position in a phrase. A whistled syllable catalog of different types and related variants was compiled in this manner (Fig. 2b). Isoglosses are lines connecting bird samples sharing the same syllable types or variants (Mundinger 1982). All bird samples sharing syllable type 1 are delineated by a line, and the groups of bird samples sharing types 2-4 are each delineated by other lines.

Song types were classified only by the whistled phrase without considering the harmonic phrase for 2 reasons. First, all songs contained the whistled phrase, but not all songs contained the harmonic phrase. Second, the presence of the harmonic phrase was variable within a bird sample from the same location, and therefore, it was unsuitable for analyzing the microgeographic pattern of songs based on the harmonic phrase. Songs were categorized as the same type if the whistled syllables were sequenced into identical motifs. To illustrate the manner in which song types were classified, consider a song consisting of 4 different syllables (each designated by a different number): 1-2-3-4. In the song categorization scheme, both syllable identity (type and variant) and order were considered; for example, 1-2-3-4 and 1-2-4-3 contain exactly the same syllables, but they are organized in different orders and would therefore be considered different song types. Song types 1-2-3-4b and 1-2-3-4d would be considered different because of different variants in the last syllable (Table 1).

Determination of the similarity score between 2 song types

Considering the small syllable repertoire (Fig. 2b) in the study population of the Grey-cheeked Fulvetta, both the order and identity of syllables played important roles in comparing song types. I calculated the similarity coefficient (Si) between 2 song types as follows:

$$Si = (Sa + 0.5 * Sb)/Sc;$$

where Sa is the number of the same syllable types or variants shared by the 2 songs in the exact same order, Sb is the number of the same syllable types but different variants shared by the 2 songs in the exact same order, and Sc is the greater number of total syllables between the 2 songs. Because different variants of the same syllable type usually share 1/2 similar notes (Fig. 2b), Sb was weighted by 0.5 before adding it to Sa. If a syllable type appeared more than once in the same song, it was counted as many times as it occurred. For example, the Si for song types 1-2-3 and 1-2-3-4 was (3 + 0.5*0)/4 or 0.75; the Si for song types 1-2-3-4 and 1a-1a-2-3-4 would be (3 + 0.5*1)/5 or 0.7 (in song 1a-1a-2-3-4: 1, 2, 3, and 4 indicate syllable types, and 1a indicates a variant of type 1). Similarity coefficients range from 0 (complete dissimilarity) to 1 (complete similarity).

A cluster analysis was constructed using a matrix of similarity scores obtained by average linkage clustering using the unweighted pair-group method (UPGMA) on the song types of 21 bird samples. A song theme was subjectively defined as a group of song types having similarity scores of greater than 0.6. This was justified by considering that the total number of whistled syllables in most songs was 4 (Table 1), and a similarity score greater than 0.6 indicated that 2 song types had at most 1 different syllable between them. I used SAS software (SAS Institute 1989) to analyze the data and MEGA version 2.1 software (Kumar et al. 2001) to draw a hierarchical phenogram.

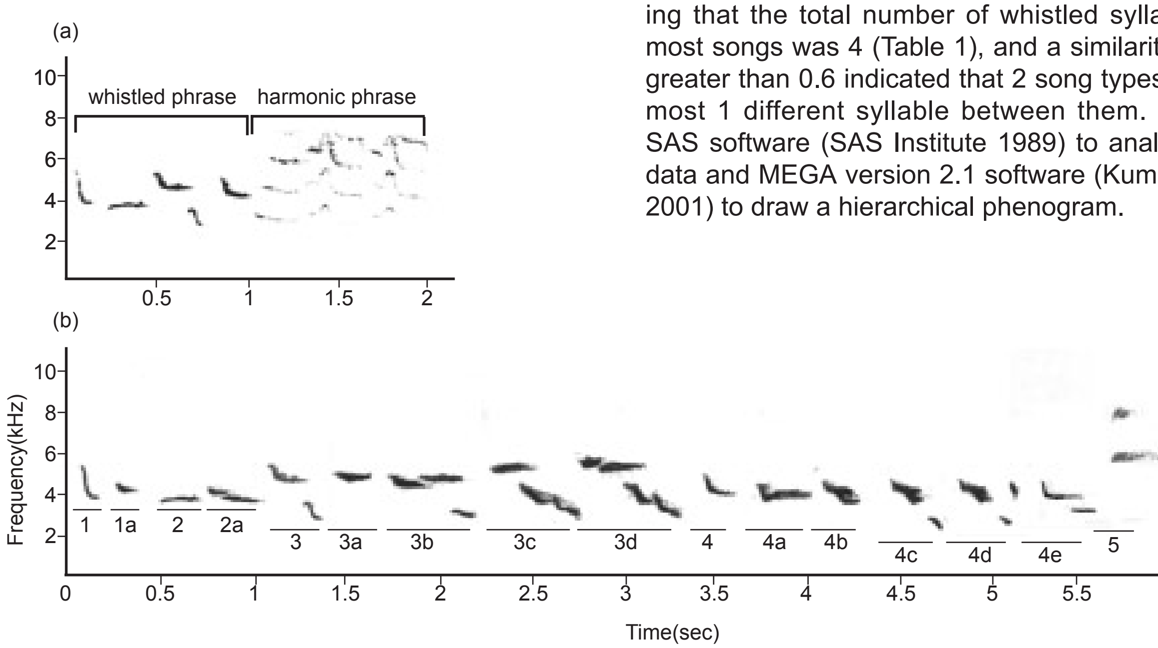

Fig. 2. Sonograms illustrating (a) the 2 phrases of Grey-cheeked Fulvetta songs recorded at Shoushan Nature Park, Kaohsiung and (b) different syllable types and variants of the whistled phrase. Syllables and variants of the whistled phrase are designated by unique identification numbers; identification numbers are shown here beneath the corresponding syllables or variants.

RESULTS

Song structure

In total, 212 songs were obtained from 21 bird samples at 19 different locations (Table 1; Fig. 1). Songs of the Grey-cheeked Fulvetta typically ranged from 2 to 8 kHz in frequency (Fig. 2a). The duration of a song ranged from 1.021 to 2.507 s (mean ± SE, 1.545 ± 0.021 s, n = 207 after discarding 5 songs with unclear harmonic phrases). The variation in the duration within a bird sample was significantly lower than the variation in the duration among bird samples (Kruskal-Wallis test, p < 0.01). The mean duration of songs within a bird sample ranged from 1.156 to 1.962 s (Table 1).

A typical song contained 2 distinct phrases, a whistled phrase and a harmonic phrase, which differed in sonogram structure and variability (Fig. 2a). The harmonic phrase ranged over a higher frequency than the whistled phrase (Fig. 2). Temp

Table 2. Temporal and spectral characteristics of syllables of songs of the Grey-cheeked Fulvetta at Shoushan Nature Park, Kaohsiung, Taiwan during March-July 2001

Syllable	No. of bird samples	[a]Mean ± SE (coefficient of variation)					
		Duration(ms)	Mean frequency (Hz)	Start frequency (Hz)	End frequency (Hz)	Maximum frequency (Hz)	Minimum frequency (Hz)
Type 1	15	98.2 ± 6.7 (26.46) ***	3728 ± 35 (3.64) ***	4785 ± 53 (4.32) ***	3599 ± 41 (4.4) ***	4830 ± 58 (4.64) ***	3539 ± 41 (4.52) ***
Type 2	17	192.8 ± 4.8 (10.18) ***	3270 ± 35 (4.35) ***	3396 ± 96 (11.67) ***	3293 ± 54 (6.76) ***	3531 ± 109 (12.71) ***	3143 ± 35 (4.57) ***
Type 3	18	307.8 ± 9.2 (12.64) ***	4467 ± 48 (4.58) ***	4717 ± 37 (3.32) ***	2888 ± 53 (7.82) ***	4817 ± 36 (3.13) ***	2781 ± 52 (7.95) ***
Type 4	15	195.2 ± 6.0 (11.94) ***	3963 ± 23 (2.24) **	4533 ± 45 (3.81) ***	3976 ± 46 (4.51) ***	4598 ± 59 (4.92) ***	3860 ± 23 (2.3) ***
Type 1a	5	100.8 ± 12.0 (26.7) ***	4117 ± 144 (7.82) ***	4378 ± 148 (7.56) ***	4030 ± 196 (10.86) ***	4413 ± 148 (7.49) ***	3968 ± 179 (10.09) ***
Type 2a	3	303.3 ± 14.5 (8.31) ***	3681 ± 96 (4.5) ***	4322 ± 85 (3.39) ***	3661 ± 84 (4.0) ***	4331 ± 93 (3.71) ***	3584 ± 59 (2.87) ***
Type 4b	3	263.1 ± 72.7 (47.83) *	4243 ± 128 (5.24) *	4591 ± 61 (2.28) ns	3790 ± 26 (1.17) ns	4659 ± 95 (3.52) *	3569 ± 165 (7.99) ns
Type 4c	2	358.3 ± 144.3 (56.96) ns	4125 ± 172 (5.89) ns	4463 ± 21 (0.65) ns	2680 ± 4 (0.2) ns	4478 ± 6 (0.2) ns	2512 ± 172 (9.66) ns
Type 3a	1	178.0	4672	4743	4770	4846	4523
Type 3b	1	460.0	4469	4281	2713	4546	2676
Type 3c	1	449.3	4974	5095	2702	5232	2846
Type 3d	1	501.0	5059	5362	2788	5437	3006
Type 4a	1	255.5	4067	4402	3946	4481	3739
Type 4d	1	303.5	4270	4673	3838	4676	2472
Type 4e	1	324.8	3954	4532	3316	4851	3106
Type 5	1	84.3	5792	5609	5770	7848	5670

***Kruskal-Wallis test, p < 0.001; **p < 0.01; *p < 0.05; ns: p > 0.05.
[a]Using bird samples as sampled units, SE and CV were calculated only for shared syllable types (n > 1).

oral structure of the harmonic phrase was more variable than that of the whistle phrase. In all recorded songs, the whistled phrase included 3-5 syllables and ranged from 0.722 to 1.651 s (1.069 ± 0.0083 s, n = 212), whereas the harmonic phrase included 0-4 syllables and ranged from 0 to 1.602 s (0.45 ± 0.0207 s, n = 207 after discarding 5 songs with unclear harmonic phrases). All recorded songs contained the whistled phrase, whereas 10.6% (22/207) of them contained no harmonic phrase.

Within a bird sample, the number of whistled syllables was consistent, whereas the number of harmonic syllables was not (Table 1). Furthermore, the duration of the harmonic phrase within a bird sample showed a greater standard error (SE) than that of the whistled phrase for all bird samples except N6 (Table 1). The mean duration of whistled phrases within a bird sample ranged from 0.794 to 1.61 s; the difference among bird samples was significant (Kruskal-Wallis test, $p < 0.01$). The mean duration of harmonic phrases within a bird sample ranged from 0.071 to 0.885 s; the difference among bird samples was also significant (Kruskal-Wallis test, $p < 0.01$).

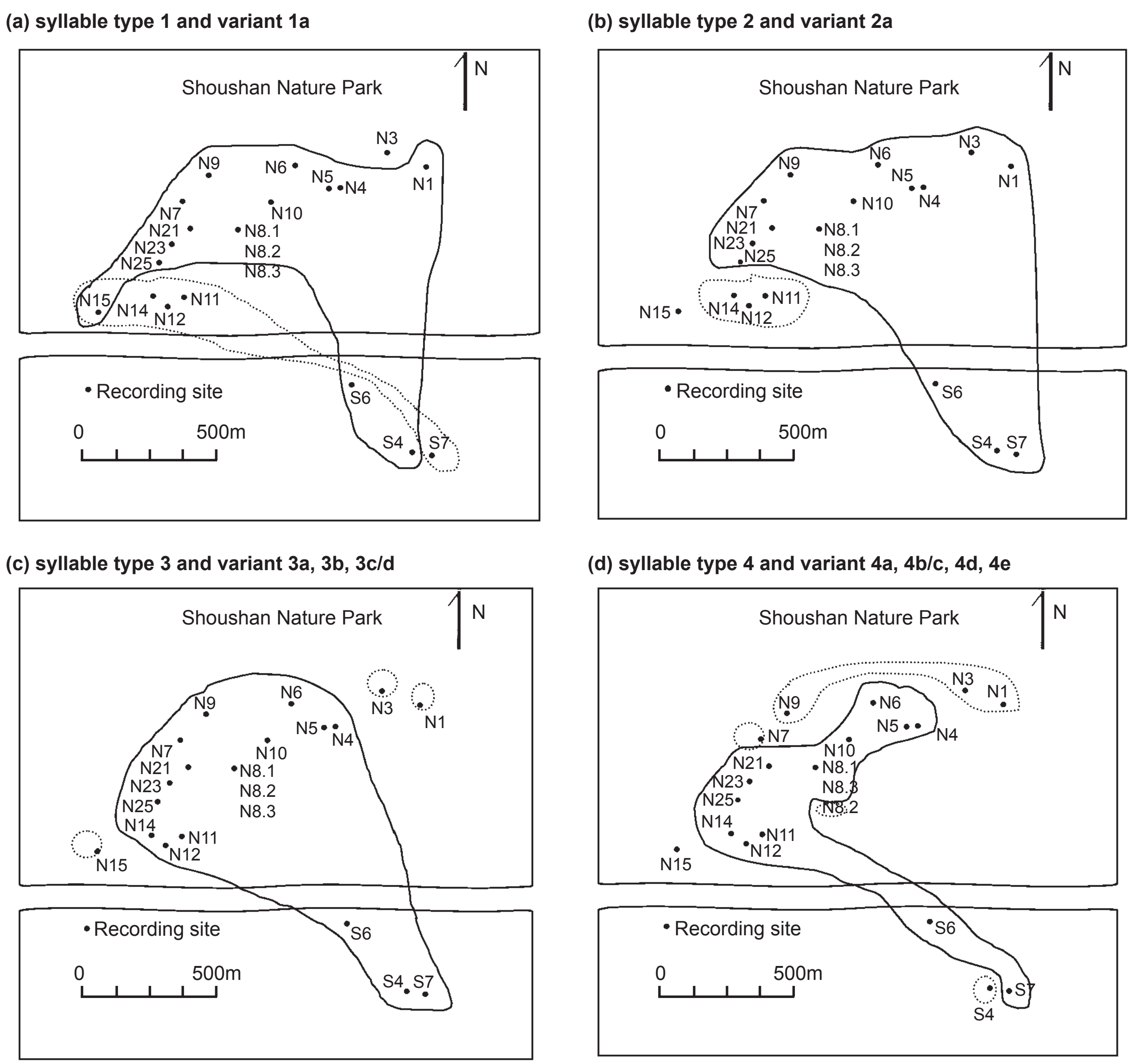

Fig. 3. Microgeographic pattern based on isoglosses of syllable types (solid lines) and their variants (dotted lines) of the whistled phrase.

Song variation

Syllable types and their related variants

Five syllable types (1-5) and 11 variants of syllable types were classified for the whistled phrase (Fig. 2b). Measurements were made on different songs of the same bird sample, and descriptive statistics were calculated using the averages of these measurements, that is, a bird sample was a sample unit (Table 2). Coefficients of variation (CVs) among bird samples for measured characters were calculated as the standard deviation divided by the mean times 100%. In shared syllable types ($n > 1$), the CV of the frequency variable was below 8% on most occasions (35/40) (Table 2). In contrast, the CV of the duration was above 8% for all shared syllable types, with some of them even having a CV above 40%.

Bird sample differences were significant for all variables of syllable types 1-4 (Kruskal-Wallis test, $p < 0.05$; Table 2). Those 4 syllable types were shared by at least 15 bird samples, and each had 1-5 variants (Fig. 2). Of the 4 syllable types, syllable type 4 had the most number of variants (Table 2). Syllable type 5, which was recorded from only 1 bird sample, had no related variants.

The zones of the 4 isoglosses, corresponding

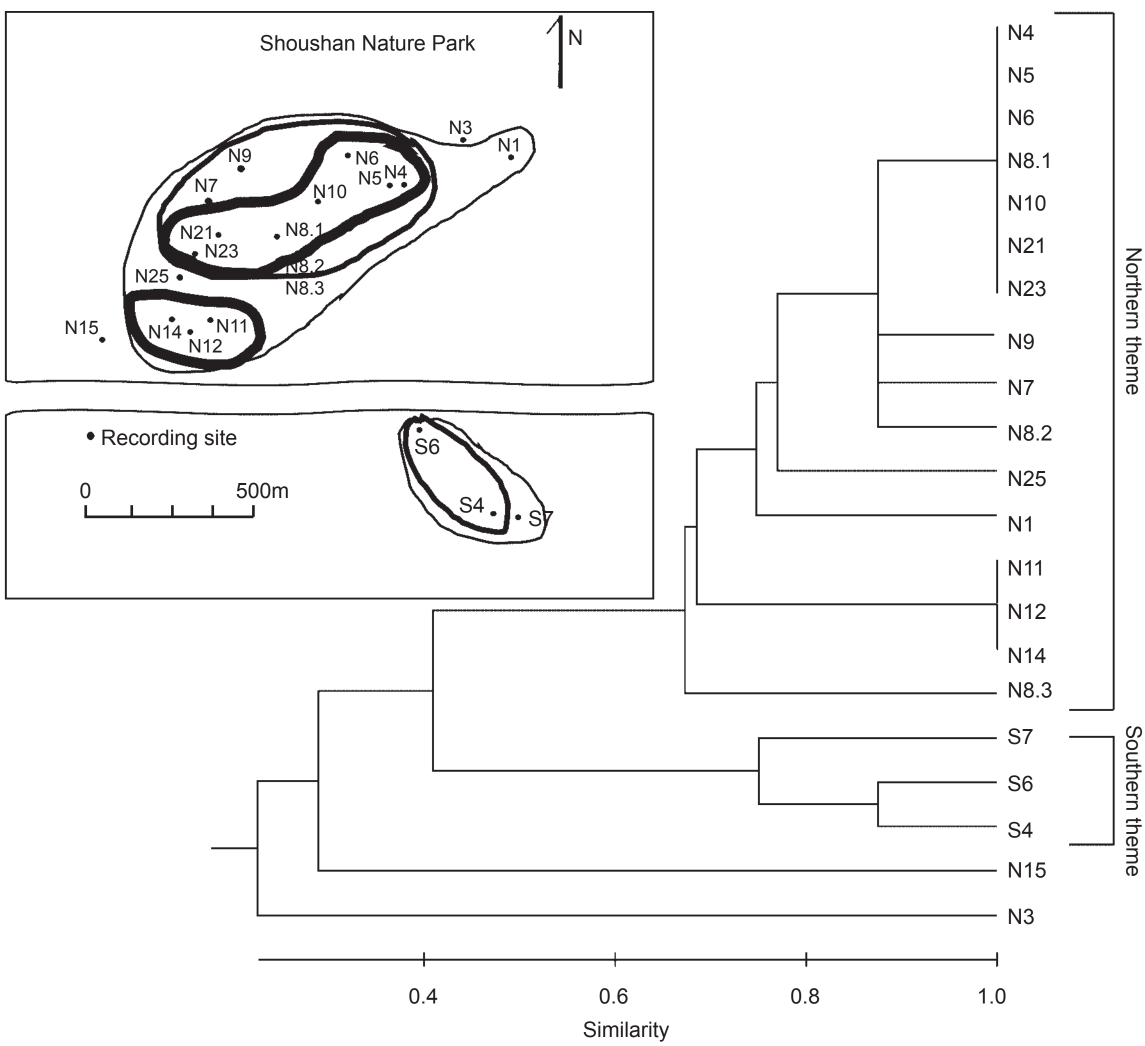

Fig. 4. Tree diagram resulting from average linkage clustering using the unweighted pair-group method (UPGMA) of songs of 21 bird samples at Shoushan Nature Park, Kaohsiung. The figure on the top left corner shows the microgeographic pattern based on the similarity analysis among song types. The thickness of the circled lines is proportional to the degree of similarity: the thickest line represents 100% similarity, the 2nd-thickest line represents > 80% similarity, and the thinnest line represents > 60% similarity.

to the 4 main syllable types (1-4), interlaced and had no discrete boundaries separating them (Fig. 3). Isoglosses of syllable type 2 and its variant 2a, however, could identify 2 separate groups with discrete boundaries (Fig. 3b). Variants were usually shown in a single bird sample and occurred at the periphery of isoglosses of their related syllable types (Fig. 3).

Song types and themes

In most bird samples (19/21), a bird sample showed only 1 stereotyped song, which may be shared by other bird samples (Table 1). In total, 15 song types were recognized in 21 bird samples from 19 different locations, and whole-song sharing occurred in 7 (song type 1-2-3-4) and 3 (song type 1a-2a-3-4) bird samples, respectively (Table 1; Fig. 1). Song type 1-2-3-4, which was shared by 1/3 (7/21) of all bird samples, could be viewed as the main song theme in the study area. Using 0.6 as a similarity criterion, the results of cluster analysis revealed 4 song themes: northern, southern, N15, and N3 (Table 1; Fig. 4). Northern theme samples were separated from southern theme samples by a discrete boundary (Fig. 4). The northern theme group was further subdivided by a minor boundary, and 2 small clusters of bird samples showed the same song types of 1-2-3-4 or 1a-2a-3-4 (Table 1; Fig. 4).

The northern theme, which was shared by 16 bird samples from 14 different locations (Fig. 4), was characterized by having the syllable sequence 1(or 0)-2-3(a)-4(b/c/d/e) in the whistled phrase. The southern theme however, which was shared by 3 bird samples from 3 different locations (Fig. 4), was characterized by having the syllable sequence 1(a)-2-4(a)-3 in the whistled phrase. The reverse order of the last 2 syllables in the whistled phrase marked the difference between the northern and southern themes.

DISCUSSION

Whistled and harmonic phrases of a song

In many bird species, song serves to repel rivals and/or attract mates (Catchpole 1982). In this study, songs of the Grey-cheeked Fulvetta contained 2 distinct phrases. The 1st phrase, the whistled phrase, is detectable by ear even from a long distance, and each bird sample had 1-2 stereotyped sequences of 3-5 syllables. The sonogram structure of the whistled phrase is tonal, and the whistle-like structure allows the sound to transmit well throughout the forest (Morton 1975, Wiley and Richards 1982). For species with short and stereotyped songs, songs are usually used for territorial advertisement and repelling others (Catchpole 1982). Therefore, it is suggested that the whistled phrase might serve to repel rivals by means of long-distance communication.

The 2nd, harmonic phrase has sonogram structures of a broad frequency range in which sounds are easily located, and higher-pitched characteristics (dominant frequency > 6 kHz), implying a non-aggressive but quickly attenuated nature (Morton 1975, Wiley and Richards 1982). Furthermore, the results show that some sampled birds varied the number of syllables in the harmonic phrase, and even sang with no harmonic phrase at all. The harmonic phrase might therefore be sung depending on different contexts such as the presence of available mates, and thus might serve for short-distance communication. The suggested dual function of songs for the Grey-cheeked Fulvetta is not unique in birds. In some warbler species with small repertoires, 2 kinds of songs function differently, one for territorial defense and the other for pair-bond maintenance (Catchpole and Slater 1995).

Microgeographic variation and local dialects

This study demonstrates that the songs of the Grey-cheeked Fulvetta are relatively stereotyped and invariable with regard to the number of syllable types in the population and size of the song type repertoire within a bird sample. Only 5 syllable types and 11 variants were found in the whistled phrase of the study population. Within a bird sample from the same location, the song types were generally quite stereotyped, with only occasional variations such as the addition or deletion of a few notes. Syllable type 4, which usually occurred in the last position of the whistle phrase, had more variants than the other syllable types. This suggests that variations generally occurred at the end of the whistled phrase.

A dialect pattern is characterized by discrete boundaries between song forms (Mundinger 1982). Discrete boundaries between song forms can be identified using certain syllable types (Baptista 1977, Ficken and Weise 1984, DeWolfe and Baptista 1995, Chilton and Lein 1996, Nelson 1998, Miyasato and Baker 1999) or song type similarity (Cicero and Benowitz-Fredericks 2000, Nelson 2000, MacDougall-Shackleton and MacDougall-Shackleton 2001). In the study population of the Grey-cheeked Fulvetta, major discrete boundaries could be illustrated based on microgeographic patterns of song type similarity instead of syllable type sharing. Two dialects distinguished by major discrete boundaries were the northern theme (recorded from 14 different locations) and the southern theme (recorded from 3 different locations). The prominent difference between the 2 song themes is the reversed order of the last 2 syllables in the whistled phrase.

Within the range of the northern theme, there were 2 subdialectal nuclei in which whole-song sharing was found in 2 clusters of neighboring samples. Discrete boundaries of these 2 subdialects could also be identified using the isoglosses of syllable type 2 and its variant 2a. The major dialects of the Grey-cheeked Fulvetta at a local level could be distinguished primarily by the order of the last 2 syllables in the whistled phrase, while the subdialects were distinguished primarily by variations of syllables.

Song dialects have been described for many passerine birds. By an earlier tabulation, about 64 to 75 species of birds have been shown to exhibit dialects (Kroodsma and Baylis 1982, Mundinger 1982). Many models of the significance and maintenance of dialect patterns have been proposed: habitat matching, genetic adaptation, social adaptation, historical processes, and geographical barriers (see Catchpole and Slater 1995 for a review). According to the historical model of dialect maintenance discussed by Baker (1975) and Payne (1981), dialects diverge with time in areas isolated by distance or geographic barriers. In the present study, which was conducted in a single area with similar habitats, habitat matching and geographical barriers do not seem to be appropriate explanations for the microgeographic patterns found in this study. Neither did the similarity of habitats in these 2 dialect ranges suggest differences in selective forces. Dispersal across a control line between 2 dialects was unrestricted, but there was a dialect boundary in the absence of a geographic barrier in the study area.

The other 2 hypotheses, genetic adaptation and social adaptation, have different assumptions about the timing of song learning relative to dispersal. The genetic adaptation hypothesis assumes that a song is learned before philopatric dispersal, with dialect boundaries acting as partial barriers to dispersal (Nottebohm 1969, Baker 1982, Cunningham et al. 1987, MacDougall-Shackleton and MacDougall-Shackleton 2001). The social adaptation hypothesis suggests that birds benefit by copying the songs of other sampled birds in an area after natal dispersal and thus produce a pattern of local dialects (Payne 1981 1982, Nelson et al. 2001). Recoveries of ringed Grey-cheeked Fulvettas have indicated that young birds disperse to several different social groups during the non-breeding season (Lin 1996). In many bird species, young birds acquire their songs through exposure to adult models during a sensitive phase early in life (Jellis 1977, Catchpole and Slater 1995). Whether birds in the study population learn songs before or after dispersal is still unclear and requires further research.

Factors involved in the cultural transmission and stability of a pool of syllable types may differ from those governing whole songs. For example, Payne et al. (1981) found that few song themes persisted for 17 years in a population of Indigo Buntings, whereas syllable types remained stable over that period of time. In contrast, Harbison et al. (1999) found that song structure remained highly consistent in large populations, and that dialects of those large populations were unaffected by extinction of syllables or invasion by foreign syllables. To understand the mechanisms and persistence of local song dialects in the Grey-cheeked Fulvetta, further research is required on the timing of song learning relative to dispersal, and changes in microgeographic variation of syllables and song types through time.

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