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Geographic variations and temporal changes in songs of the Rufous-capped Babbler (*Stachyris ruficeps praecognita*)

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Song has been an important subject in studying geographic variation and cultural evolution across bird populations, but the quantitative analysis of song has been problematic. The aim of this study is to investigate the temporal changes and geographic variations in songs of Rufous-capped Babblers (*Stachyris ruficeps praecognita*) using both spectrographic cross-correlation (SPCC) analysis and multivariate analysis on spectrographic measures. We recorded songs at Shoushan Nature Park of southern Taiwan from 2001 to 2004 and five other sites including Fushan in northern Taiwan, Sun Moon Lake in central Taiwan, and Gauchon, Sanpin, Nazenshan in southern Taiwan. The results showed that the cross-correlation coefficients of songs between bird samples were relatively smaller than those within samples. Using SPCC analysis on first notes instead of whole songs, songs of northern Taiwan could be differentiated from those of central or southern Taiwan. Results of multivariate analysis on spectrographic measures showed that mean frequency, minimum frequency and maximum frequency of the first note were the primary acoustic parameters responsible for this differentiation. However, there were no obvious patterns of temporal changes of songs in the habitat island population of Shoushan Nature Park, which could have resulted from higher variations among individuals within the same year in this high density population. We conclude that the SPCC analysis works as a starting point to examine the geographic variations in songs with simple structures and a following mutivariate analysis is effective in identifying the acoustic parameters resulting in those geographic variations.

1. Introduction

Geographic variation in song has been well studied and found in many bird species (Catchpole & Slater 1995). It has important implications for many aspects of the ecology of bird populations (Kroodsma & Miller 1996). In studying the geographic variations in bird songs, it is critical to detect similarities and differences among songs from individuals of the same area or different areas. There are three commonly used methods to quantify the similarities of sounds: (1) comparison of sounds by a set of measured acoustic parameters (multivariate method), (2) comparison of sound spectrograms by spectrographic cross-correlation (SPCC) analysis, and (3) visual comparison of sound spectrograms by a human observer (Cortopassi & Bradbury 2000).

Visual inspection is a widely used method for classifying complex sounds groups and work quite well for those songs with complex structures (Payne *et al*. 2000). However, for songs with similar notes heard the same or seen the same on spectrograms through a human observer, the method of visual comparison is inadequate. Alternatively, the SPCC analysis could be used not only for simple sounds with no significant overtone content (Khanna *et al*. 1997), but for harmonically rich sounds as well (Cortopassi & Bradbury 2000). The SPCC analysis developed by Clark *et al*. (1987) compares the time-frequency spectrograms of two sounds, and takes the peak correlation value as a measure of sound similarity. The intent of the SPCC analysis is to include all structural features of the two sound spectrograms instead of limiting comparison to a predetermined and possibly incomplete set of measures. Although the SPCC analysis has the advantage that it considers the entire sound objectively, care has to be taken with the sound types being compared, the amount of noise in the signal, and with the settings used to create the spectrograms because these factors will affect the similarity value generated (Khanna *et al*. 1997, Latruffe *et al*. 2000, Terry *et al*. 2001, Terry *et al*. 2005). Furthermore, the results of SPCC only contained the similarity value without giving any information about how two sounds differ in terms of acoustic features. In contrast, the multivariate method based on a set of measured acoustic parameters has been applied successfully to compare songs with few kinds of notes (Payne 1978, Trainer 1983, Clark *et al*. 1987, Shackell *et al*. 1988, Gaunt *et al*. 1994, Khanna *et al*. 1997, Bell *et al*. 1998), and also show how two sounds different in terms of those measured parameters. The disadvantage of the multivariate method is that it still has the subjectivity and limitation in selecting the measured acoustic parameters for analysis.

The Rufous-capped Babbler (*Stachyris ruficeps praecognita*) is a resident endemic subspecies commonly found in lowland forests of Taiwan. In the non-breeding season, Rufous-capped Babblers usually forage with Grey-cheeked Fulvettas (*Alcippe morrisonia morrisoniana*) and form mixed-species flocks (Chen & Hsieh 2002). Males of Rufous-capped Babblers look similar to females without sexual dimorphism. Two kinds of sounds have usually been described verbally in the Rufous-capped Babbler: the "ju-ji" call and the "du-du-du-du-du-du-du" song. In comparison with other complex bird songs, the songs of Rufous-capped Babblers contain only simple whistle-like structures, and visual classifications were not indicated as appropriate in our analysis.

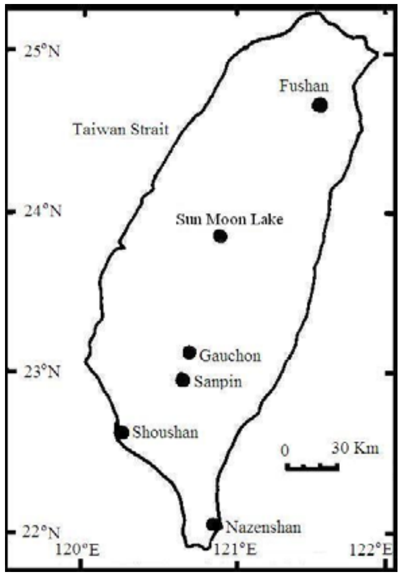


Fig. 1. Map of recording sites in Taiwan.

In this study, we used the two analytical methods (SPCC and multivariate methods) in measuring similarity of songs to achieve the following objectives: (1) to determine if different populations of the Rufous-capped Babbler, whether geographically or temporally, show evidence of differentiation of songs, and (2) to evaluate the ability of the two analytical methods to document any such differentiation.

2. Material and methods

2.1. Field Populations and Song Recordings

Songs of Rufous-capped Babblers were recorded in the field using a Denon Portable IC Recorder (DN-F20R) equipped with a Sennheiser ME 67 shotgun microphone. All recordings were obtained between 06:00 and 11:00 in the morning.

We recorded songs of an individual until it either stopped singing or flew out of recording range. Songs recorded from the same individual were classified into one bird sample. Because the birds were not individually marked, songs recorded from different locations or different years were regarded as from different individuals, and thus were classified into different bird samples. Songs were collected at six sites of Taiwan during March–July in different years: Nazenshan in 2001, Sanpin in 2002, Gauchon in 2003, Fushan in 2003, Sun Moon Lake in 2003, and Shoushan Nature Park in 2001–2004 (Fig. 1). Songs sampled from the population of Shoushan Nature Park were analyzed separately from those of the other five sites because the population is situated on a habitat island surrounded by unsuitable habitats of urban areas and the sea. The area of Shoushan Nature Park is about 1000 ha and situated in Kaohsiung City of southern Taiwan.

2.2. Song Comparisons and Similarity Scores

Songs were analyzed using Avisoft-SASLab Pro Package (Raimund Specht, Berlin, Germany; with a sampling rate of 22.05 kHz and a sample size of 16 bits) (Specht 2002). We made spectrograms from selected, good-quality songs that were high-pass filtered (FIR-Filter) at 1.5 kHz to remove low frequency noise. Spectrograms were prepared with the following settings: frequency resolution 43 Hz and time grid resolution 2.9 ms with FFT-length of 512 points, Frame size of 100%, Temporal overlap of 87.5% and Hamming window.

We used the Avisoft-CORRELATOR computing the spectrographic cross-correlation (SPCC) coefficients, and a triangular matrix of the similarity scores was determined by pairwise comparisons of the selected spectrograms. The SPCC coefficient (range 0–1) represents the peak similarity scores obtained between two sounds. In the Avisoft-CORRELATOR, an additional sliding in frequency can be specified if small frequency deviations of the signals should be ignored (Tolerate Frequency-Deviation function) (Specht 2002). In this case, the two spectrograms to be correlated will be slid additionally along the frequency axis in order to find the true peak similarity. In this study, a tolerating frequency deviation was initially set at

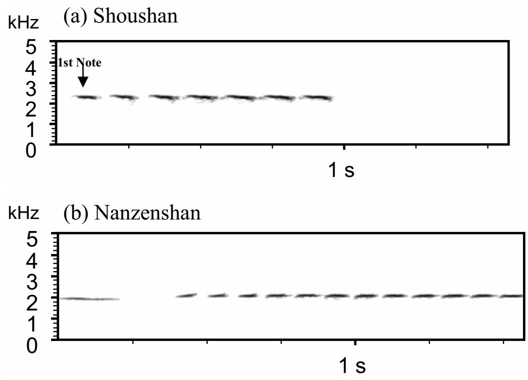


Fig. 2. Spectrograms of example songs of Rufous-capped Babblers from (a) Shoushan Nature Park and (b) Nanzenshan.

100 Hz, which took 4–5 times of recalculations because of 43 Hz frequency resolution. The similarities of the selected spectrograms were averaged and then recalculated each time after adding 100 Hz to the tolerating frequency until the average reached its maximum value at which the optimal tolerating frequency deviation was determined. Because the whole songs may be too long to obtain a high similarity score in comparisons and the first notes of the songs also appeared different among bird samples by preliminary visual examination on the spectrograms, the above analyses were done on spectrograms of both the whole song and the first note of a song respectively (Fig. 2).

We compared songs within a bird sample and songs between bird samples. One clear representative spectrogram of either the whole song or the first note of a song from each bird sample was selected for the SPCC in comparing between sites, across years, and for the following multivariate analysis. Clustering patterns of bird samples were examined by using the cluster analysis and non-metric multidimensional scaling (MDS) ordination on the similarity matrix of the selected comparisons. MDS is an often used ordination technique for exploring similarities in samples visually (Clarke & Warwick 1994). The purpose of using MDS in this study is to picture the bird samples as points in 2-dimensional space such that relative distances apart of all points are in the same rank order as the relative similarities of the samples (as calculated by SPCC in this case). Close points represent bird samples that are very similar in spec-

Table 1. Definitions of acoustic parameters measured on the spectrograms of the songs of the Rufous-capped Babbler (*Stachyris ruficeps praecognita*).

Acoustic parameter	Definition
Dur	Duration of the song
Freq	Frequency of the maximum amplitude derived from the mean spectrum of entire song
Min	Minimum frequency derived from the mean spectrum of entire song
Max	Maximum frequency derived from the mean spectrum of entire song
Range	Frequency range of the song (= Max–Min)
FNDur	Duration of the first note
FNFreq	Frequency of the maximum amplitude derived from the mean spectrum of the first note
FNMin	Minimum frequency derived from the mean spectrum of the first note
FNMax	Maximum frequency derived from the mean spectrum of the first note
FNRange	Frequency range of the first note (= FNMax–FNMin)
Int	Interval between the first note and the second note
NNote	Number of notes

trograms. The adequacy of 2-dimensional MDS can be assessed by the stress values calculated by Primer 5.0 (Clarke & Gorley 2001). It is suggested that stress values < 0.1 corresponds to a good ordination without misleading interpretation and stress values 0.1–0.2 gives a potentially useful 2-dimensional picture (Clarke & Warwick 1994).

For the multivariate analysis, acoustic parameters (Table 1, Fig. 2) on representative spectrograms were measured using automatic parameter measurement setup in Avisoft-SASLab Pro (Specht 2002). Then, Principal Component Analysis (PCA) was performed using Primer 5.0 on measurements of all song samples with normalized transformation. In performing PCA, we combined song samples from Shoushan Nature Park and other five sites to ensure enough samples analyzed for 12 parameters.

3. Results

3.1. Spectrographic Cross-correlation (SPCC)

In total, 352 songs of the Rufous-capped Babbler were recorded from 76 bird samples at six different sites. For songs within a bird sample, pairwise cross-correlation coefficients were calculated. The average of coefficients of songs within a bird sample ranged from 0.67 to 0.93, and the CV ranged from 1.7% to 14.8% (Table 2). The cross-correlation coefficients of songs between bird

Table 2. Ranges of variations in cross-correlation coefficients of songs within a bird sample.

Sources of samples	Mean range	CV range	Number of songs measured in a bird sample
Shoushan 2001	0.67–0.9	2.1–14.8%	2–10
Shoushan 2002	0.82–0.9	3.2–8.1%	3–22
Shoushan 2003	0.7–0.89	3.3–12.7%	2–9
Shoushan 2004	0.69–0.89	3.7–9.9%	2–15
Sanpin	0.82–0.86	3.9–5.4%	3–9
Gauchon	0.72–0.93	1.7–12.8%	2–14
Naizenshan	0.79–0.89	4.9–14%	5–13
Sun Moon Lake	0.68–0.77	7–8.2%	3–5
Fushan	0.81–0.84	2.6–10%	4–15

Table 3. Variations in cross-correlation coefficients of songs between bird samples

Sources of samples	Tolerate frequency deviation (Hz)	Coefficient mean	CV (%)	Number of bird samples
Shoushan 2001	0	0.32	72.3	22
Shoushan 2002	0	0.4	53.4	9
Shoushan 2003	0	0.45	37.8	11
Shoushan 2004	0	0.39	47.4	15
Other Sites*	0	0.37	52.7	19
Total	0	0.36	56.4	76
Shoushan 2001	300#	0.62	16.6	22
Shoushan 2002	200#	0.68	11.6	9
Shoushan 2003	100#	0.57	14.5	11
Shoushan 2004	200#	0.60	12.3	15
Other Sites *	200#	0.61	12.1	19
Total	200#	0.61	13.6	76

* Including Sanpin, Gauchon, Naizenshan, Sun Moon Lake, and Fushan.
\# The tolerate frequency-deviation at which the cross-correlation coefficient has the greatest mean.

samples were much smaller than those within a bird sample. For songs between bird samples, the coefficient mean was 0.32 to 0.45 in Shoushan, and 0.37 in other sampled sites; the CV increased up to 37.8–72.3% in Shoushan, and 52.7% in other sampled sites (Table 3). However, after using tolerating frequency-deviation in SPCC analysis, the coefficient mean of songs between bird samples increased from 0.36 to 0.61, and the CV decreased from 56.4% to 13.6% for total samples considered (Table 3). The optimal tolerating frequency deviation ranged from 100 to 300 Hz (Table 3).

In the MDS plots for SPCC analysis on whole songs, no differentiations were found on yearly samples of Shoushan Nature Park or samples of the other five recording sites (Fig.3). Furthermore, in the MDS plots for SPCC analysis on the first notes of songs from the Shoushan Nature Park, no

Table 4. Results of principal component analysis on songs of the Rufous-capped Babbler (*Stachyris ruficeps praecognita*).

Variable	Eigenvectors			
	PC1	PC2	PC3	PC4
Dur	0.111	**0.411**	0.204	**–0.495**
Freq	–0.32	–0.372	0.173	–0.183
Min	–0.281	**–0.404**	–0.083	–0.346
Max	–0.395	–0.203	0.352	–0.052
Range	–0.206	0.193	**0.553**	0.305
FNDur	0.132	–0.095	**0.442**	0.007
FNFreq	**–0.432**	0.155	–0.15	–0.005
FNMin	**–0.42**	0.097	–0.129	–0.144
FNMax	**–0.423**	0.261	–0.09	0.111
FNRange	–0.194	0.361	0.018	**0.426**
Int	0.073	0.22	**0.457**	–0.357
NNote	–0.083	**0.403**	–0.24	**–0.404**
Eigenvalues	4.24	2.47	1.44	1.37
Cumulative% variation	35.3	55.9	67.9	79.3

Eigenvectors >0.4 are shown in boldface.

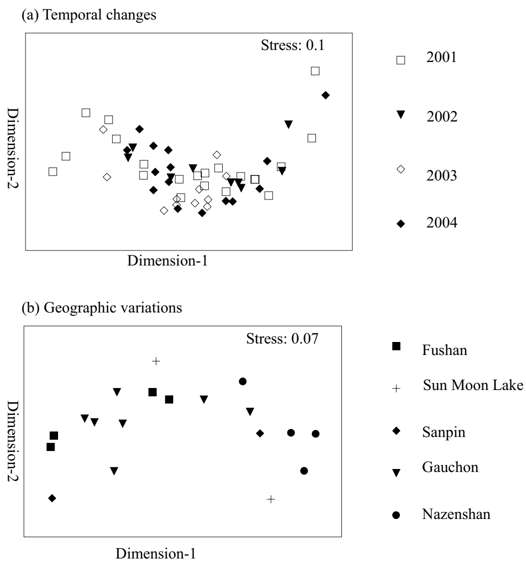


Fig. 3. Non-metric multi-dimensional scaling (MDS) plots for (a) temporal changes and (b) geographic variations using cross-correlations on whole songs. The 2-dimensional MDS plots were obtained by using the similarity matrices of cross-correlation coefficients of songs from Shoushan Nature Park (for temporal changes) and from five other sites of Taiwan (for geographic variations), respectively.

differentiations were found on yearly samples either (Fig. 4). Nevertheless, in the MDS plots for analysis on the first notes of songs from the other five recording sites, samples from Fushan could be grouped together and differentiated from samples of central or southern sites in Taiwan (Fig. 5).

3.2. Parametric Measurements

In using 12 acoustic parameters (Table 1) for principal component analysis on spectrograms of all samples, only the first four components displayed eigenvalues greater than 1, and the first two components together accounted for 55.9% of the total variance (Table 4). The PC1 was largely affected by three parameters, mean frequency of the first note (FNFreq), minimum frequency of the first note (FNMin), and maximum frequency of the first note (FNMax). In the scatter plots of PC1 vs. PC2, samples of Shoushan Nature Park from different years were interspersed and no differentiations were found (Fig. 6a). However, in the scatter

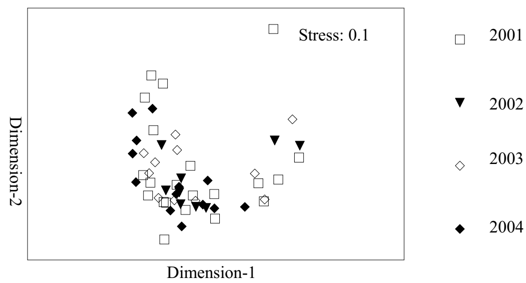
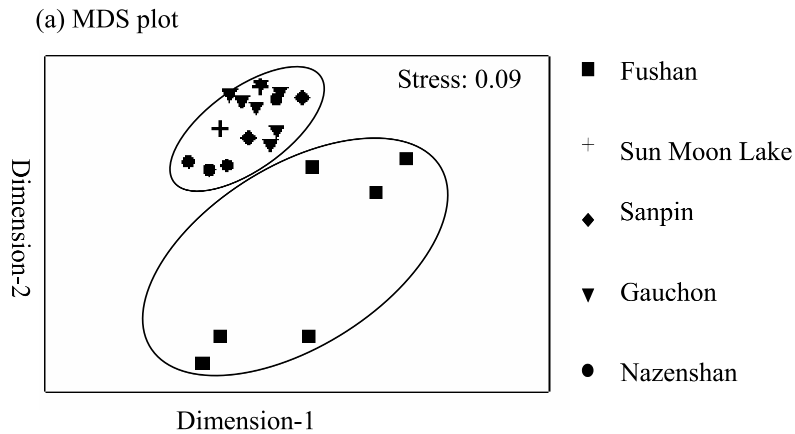


Fig. 4. Non-metric multi-dimensional scaling (MDS) plot for temporal changes in songs of the population at Shoushan Nature Park by using cross-correlation analyses on first notes of songs. The 2-dimensional MDS plots were obtained from the similarity matrix of cross-correlation coefficients.

plots of PC1 vs. PC2 for samples from other five sites, the cluster of samples from Fushan was separated from the cluster of samples from central or southern sites (Fig. 6b). Furthermore, FNFreq, FNMin, and FNMax of songs from Fushan (FNFreq: Mean $\pm$ SE = 2446.7 $\pm$ 89.8 Hz; FNMin: 2328.3 $\pm$ 70.8; FNMax: 2740 $\pm$ 83.5 Hz) were significantly higher than those from central-southern sites (FNFreq: 2057.3 $\pm$ 24.9 Hz; FNMin: 1970.7 $\pm$ 20.7; FNMax: 2229.3 $\pm$ 27.9 Hz) (t-test, FNFreq: $t1_9 = 5.76$, $P < 0.01$; FNMin: $t1_9 = 6.59$, $P < 0.01$; FNMax: $t1_9 = 7.54$, $P < 0.01$).

4. Discussion

This study has revealed three important aspects. First, both SPCC and multivariate methods demonstrated that songs recorded from Rufous-capped Babblers of northern Taiwan could be grouped and differentiated from those of central or southern Taiwan. Furthermore, it is noted that frequency of the first note of a song is the primary feature responsible for the differentiation and can be used for identifying the dialects of the Rufous-capped Babbler in Taiwan. In White-crowned Sparrows (*Zonotrichia leucophrys*), although researchers could define different dialects based on the terminal trill portion of a song (Baptista 1977), playback experiments proved that territorial males used the first parts of songs to recognize dialects (Thompson & Baker 1993). The first note of a Rufous-capped Babbler song has whistle-like structure similar to the introductory part of a White-



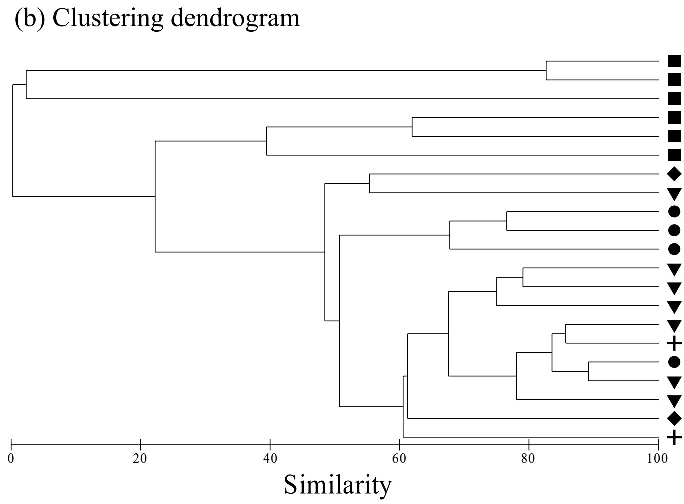


Fig. 5. Geographic variations in songs from five different sites of Taiwan by using cross-correlation analyses on first notes of songs: (a) non-metric multi-dimensional scaling (MDS) plot, and (b) clustering dendrogram. The 2-dimensional MDS plot and dengrogram were obtained from the same similarity matrix of cross-correlation coefficients.

crowned Sparrow song. We predict that Rufous-capped Babblers will distinguish northern songs from central or southern songs based on the first note in future playback experiments.

Second, our study showed that songs within a bird sample were similar with a high SPCC coefficient and a low CV; in contrast, songs between bird samples were more varied with a high CV (>30%). Although we did not mark individuals, different bird samples that were recorded at different locations or from different time periods had a great possibility of being from different individuals. If a bird sample represents an individual, the high variation of coefficients between bird samples indicates high individual variation. After using tolerating frequency-deviation in SPCC analysis, the CV of coefficients in the same sites could be largely decreased and the optimal tolerating frequency deviation ranged 100–300 Hz. This indicated that individuals of Rufous-capped Babblers in the same site sang differently from each other by the frequency of the first note of the song and this frequency difference ranged 100–300 Hz. For species with relative simple single-type songs, this frequency shift is quite common among individuals and may have important implications. Osiejuk *et al*. (2005) found that in the Ortolan Bunting (*Emberiza hortulana*), homologue syllables (syllables of the same shape) of different males had a similar bandwidth but shifted minimal and maximal frequencies, and this frequency shift is not affected by the body size variation of males. Fre-

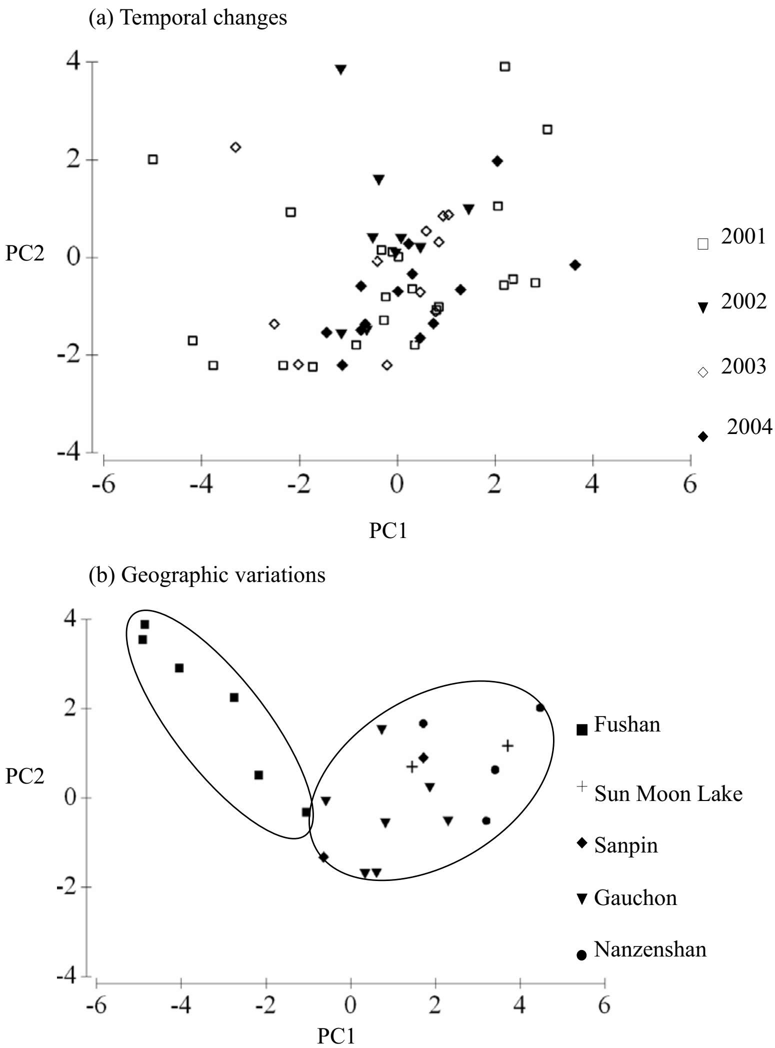


Fig. 6. Scatter plots for (a) temporal changes in songs of the population at Shoushan Nature Park and (b) geographic variations in songs from five different sites of Taiwan by using the first two components derived from a set of acoustic parameters of songs of the Rufous-capped Babbler (*Stachyris ruficeps praecognita*).

quency shift may be used to match the frequency of rival songs (Morton & Young 1986, Shackelton *et al*. 1991, Shackelton & Ratcliffe 1994, Naguib *et al*. 2002) or to indicate male quality (Christie *et al*. 2004) (review by Osiejuk *et al*. 2005). Frequency variation of homologue syllable in males is functionally significant; different frequency versions of the same type were treated as different song types (Osiejuk *et al*. 2005). The functions of frequency shifts in the Rufous-capped Babbler need special attention in future studies.

Third, no differentiated patterns of temporal changes in songs of the Rufous-capped Babblers were found in the habitat island Shousan Nature Park by using the two analytical methods. We suggested that this could have resulted from higher variations in songs of individuals within a year than those among years in this habitat island population. Based on SPCC analysis results (Table 3), the CV of cross-correlation coefficients in songs of the habitat island population for different years was not always less than that of the other five sites combined, indicating that individual variations in songs of the habitat island population were not less than that of the other five sites combined. This observation is not concordant with what the founder effect hypothesis of songs (Mundinger 1975) has suggested. The founder effect hypothesis predicts that island populations have less song variations because of the population bottleneck resulting from younger birds having fewer kinds of songs to learn from (Nottebohm 1969, Mundinger 1975, Baptista & Johnson 1982, Miller 1982, Baker & Jenkins 1987). This hypothesis has been supported by the study of fox sparrows (*Passerella iliaca*), in which less vocal variety in an isolated population has been found compared with the mainland populations (Naugler & Smith 1991). Nevertheless, Lynch & Baker (1993) argued that a higher population density plus relaxed selection for distinctive songs in the simple community of islands could lead to higher diversity in songs. According to the survey conducted by R.-Y. Tseng (unpublished data), the Shoushan population density of Rufous-capped Babblers can be up to 22.8 per ha during winter and 6.1 per ha during the breeding season. Furthermore, the Shoushan population has remained effectively isolated for the reason that the Rufous-capped Babbler is a resident species without seasonal migration and in none of the green habitats (parks) near Shoushan have any Rufous-capped Babblers been found. Thus, we suggested that the population of the Shoushan Nature Park, being an island population, could possess simple songs that vary greatly from individual to individual because of a high population density.

In conclusion, the SPCC method is useful in distinguishing dialects of the Rufous-capped Babbler, and multivariate methods based on measured parameters can be used for identifying sound characteristics responsible for the differentiation. For bird species like the Rufous-capped Babbler with songs of simple structures, the SPCC and multivariate methods are proved to be complementary and effective in examining the geographic variations in songs.

Ruostepäätimalin laulun alueellista ja ajallista vaihtelua

Laululla on ollut tärkeä rooli tutkittaessa lintupopulaatioiden alueellista vaihtelua ja kulttuurievoluutiota. Laulun kvantitatiivinen analysointi on silti ollut hyvin ongelmallista. Työmme tarkoituksena oli tutkia ruostepäätimalin laulun ajallista ja alueellista vaihtelua analysoimalla nauhoitteiden spektrografisia ominaisuuksia. Näytteet nauhoitettiin Shoushanin luonnonpuistossa Etelä-Taiwanissa sekä viidessä muussa kohteessa Pohjois-, Keski- ja Etelä-Taiwanissa vuosien 2001–2004 aikana. Analyysit osoittivat, että samalta alueelta nauhoitetut näytteet muistuttivat enemmän toisiaan kuin eri alueilta nauhoitetut näytteet.

Analysoituamme näytteistä ainoastaan ensimmäisen nuotin koko laulun sijaan, erottuivat Pohjois-Taiwanin näytteet muista näytteistä. Ensimmäisen nuotin keskimääräinen, alin ja ylin taajuus vaikuttivat näytteiden eroavaisuuksiin. Ruostepäätimalien laulu ei vaihdellut ajallisesti Sohushanin kansallispuistossa. Tämä tulos saattaa osittain johtua laulun suuresta yksilöllisestä vaihtelusta. Esittämämme analyysimenetelmät toimivat yleisenä lähtökohtana laulun alueellisten vaihteluiden selvittämisessä. Monimuuttujamallinuksen avulla on mahdollista selvittää yksityiskohtaisesti ne akustiset parametrit, joista alueelliset eroavaisuudet syntyvät.

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