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Geographic Variation of the Highly Complex Hwamei (*Garrulax canorus*) Songs

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Hsiao-Wei Tu and Lucia Liu Severinghaus (2004) Geographic variation of the highly complex Hwamei (*Garrulax canorus*) songs. *Zoological Studies* **43**(3): 629-640. Different songs in the same species may lead to reproductive divergence and potential speciation. Our aim was to compare the geographic variation of Taiwan and Mainland Hwamei (*Garrulax canorus taewanus* and *G. c. canorus*) songs both micro- and macrogeographically. Taiwan Hwamei is found only in Taiwan, while the Mainland Hwamei is found in both southern China and Indochina. We taperecorded 229 songs of 20 Taiwan Hwamei and 227 songs of 20 Mainland Hwamei, and compared them at the note, syllable, song, and syntax levels. Our results show that geographic variation of Hwamei songs mainly occurred at the syllable level and above. Mainland Hwamei shared more syllables and syntax between and among sample locations than did the Taiwan Hwamei. Mainland Hwamei songs were more complex than Taiwan Hwamei songs, containing significantly more syllable types, more variations in syllable changes, larger syntactic combinations, and fewer repeated syllables per song. The simpler songs of the Taiwan Hwamei could be a result of either the founder effect or a vicariant event.
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Key words: Taiwan Hwamei, Mainland Hwamei, Bird song, Geographic variation.

Song is a key component of territorial defense, mate attraction, and reproductive stimulation of mates among passerines (McGregor and Krebs 1982). Song differences may prevent the hybridization of species that could otherwise produce viable and fertile offspring (Grant and Grant 1997, Baker and Boylan 1999). Therefore, species-specific songs can be an important isolating mechanism among bird species (Payne 1986, Grant and Grant 1996). Different songs in the same species may lead to reproductive divergence and potential speciation (Baker and Mewaldt 1978). Studying the geographic variation of bird songs can provide information on the extent of interaction among individuals in different locales (Kroodsma 1996) and on the possible evolutionary processes the populations had experienced (McCracken and Sheldon 1997, Baptista and Krebs 2000).

Variations in bird songs have been examined either micro- or macrogeographically (sensu Mundinger 1982). Factors attributed to causes of geographic variation in bird songs include environmental variations (Morton 1975) and genetic differences (Marler and Pickert 1984, Kroodsma and Canady 1985, Baptista 1996). Song variation may also result from miscopying during the learning process (references cited in Mundinger 1982, Nelson and Marler 1994, MacDougall-Shackleton and MacDougall-Shackleton 2001).

Previous studies of geographic variation in bird songs often examined the geographic patterns of whole songs or compared song repertoire sizes of different populations. However, bird songs usually have a hierarchical structure: repertoires are composed of different songs, songs are made up of phrases, phrases have strings of distinctive syllables, and syllables are made up of notes (Catchpole and Slater 1995). Different song levels may be affected by different factors and result in different patterns of geographic variation (Tracy and Baker 1999). How notes are organized

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into syllables, and how syllables are arranged into songs may also vary geographically (Mundinger 1982, Balaban 1988). Analyzing only the higher levels in the song hierarchy may overlook variations of finer structures, but few studies have analyzed all the features of bird songs.

Our study focused on the Hwamei (*Garrulax canorus*), a drab laughingthrush living in dense undergrowth and known for its sustained singing and diverse vocalizations. This species is common in southern China and Indochina (Mainland Hwamei, *G. c. canorus*), Hainan I., China (Hainan Hwamei, *G. c. owstoni*), and Taiwan (Taiwan Hwamei, *G. c. taewanus*) (Cheng 1987, Robson 2000) (Fig. 1A). The Taiwan Hwamei can easily be distinguished from the other 2 subspecies by the lack of a white eye-ring and eye-line. The natural distributions of the 3 subspecies do not overlap, however caged Mainland Hwamei have escaped or been released and have established themselves in Taiwan since the 1980s, and hybrids between the 2 subspecies have been reported by bird watchers (Mao 1996, CH Wang and CT Lien, pers. comm., LL Severinghaus, pers. observ.). Hybrids can be identified by their incomplete white eye-ring and eye-line (Fig. 2). The island-mainland distribution and the long, complex song make this an ideal species for the study of geographic variation of bird songs. Our aim was to compare the geographic variation of Taiwan and Mainland Hwamei songs both micro- and macrogeographically at the note, syllable, song, and syntax levels. Comparing the songs of these 2 subspecies will also provide a baseline useful for future studies of the evolution of vocal communications upon secondary contact, given the fact that Mainland Hwamei and Taiwan Hwamei now hybridize in Taiwan.

METHODS

Song tape-recording

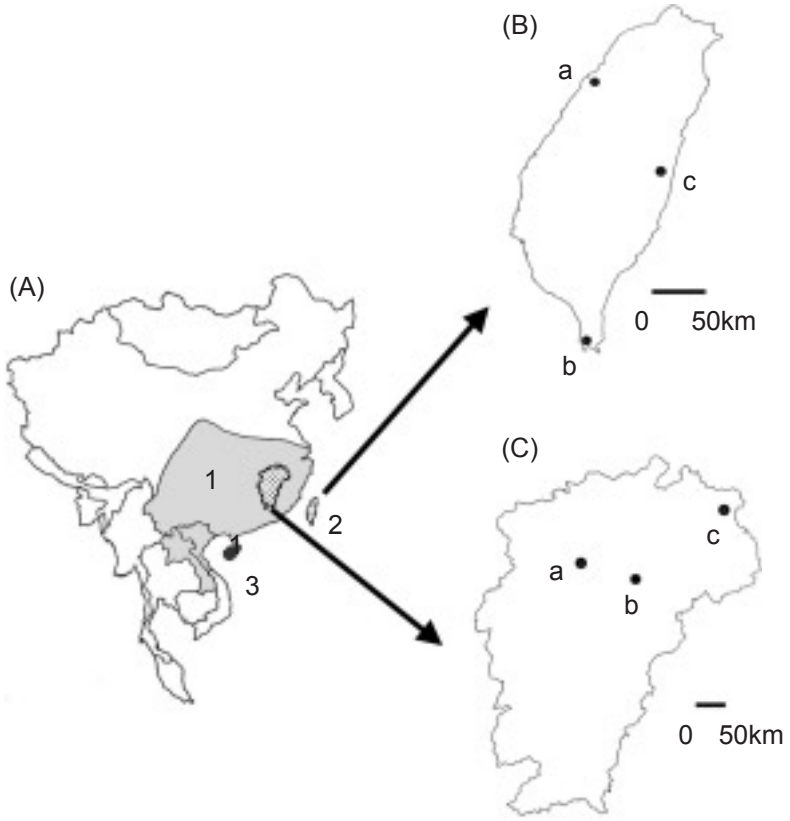

Fig. 1. (A) Distribution of Hwamei (*Garrulax canorus*). (1) Mainland Hwamei (*G. c. canorus*); (2) Taiwan Hwamei (*G. c. taewanus*); (3) Hainan Hwamei (*G. c. owstoni*). The dotted area in the range of the Mainland Hwamei is Jiangxi Province, where we sampled the songs of Mainland Hwamei. (B) Sample locations for Taiwan Hwamei songs: (a) Miaoli; (b) Pingtung; and (c) Hualien. (C) Sample locations for Mainland Hwamei songs: (a) Hualin; (b) Yunshan; and (c) Wuyuan.

All songs used in this study were tape-recorded on TDK digital audiotapes using a Sony TDC-D10 Pro II digital recorder and a Sennheiser MKH 816 directional microphone. We recorded the songs of Taiwan Hwamei from Miaoli (northwestern Taiwan), Pingtung (southwestern Taiwan), and Hualien (east-central Taiwan) Counties in Apr. 2001, and Jan. and Feb. 2003, respectively. Distances between locations were 351 km between Miaoli and Hualien, 195 km between Miaoli and Pingtung, and 279 km between Hualien and Pingtung (Fig. 1B). The songs of Mainland Hwamei were recorded by our colleagues CT Liang and CK Lee in May 2001 at Hualin, Yunshan, and Wuyuan, Jiangxi Province, mainland China. The distances were 94 km between Hualin and Yunshan, 253 km between Hualin and Wuyuan, and 189 km between Yunshan and Wuyuan (Fig. 1C). Within each sample site, we drove around and stopped at suitable habitats to look for Hwameis. Recording locations were at least 1 km apart.

Hwamei are strongly territorial and remain in pairs year round. The breeding season begins in Feb. in southern Taiwan, and in Apr./May in northern and eastern Taiwan and in Jiangxi. All songs used in this report are assumed to have served the same function of territorial defense, because all songs were induced by playing back a taped Hwamei song at the beginning or the early part of the breeding season. We found no hybrids at our sampling sites since we lured every singer into view for species identification. Thus, no hybrid songs were used in our analyses. For each bird, we recorded all of its songs until it either stopped singing or flew away. To avoid recording the same bird twice, we recorded only 1 individual per recording location, except when we were certain that the 2nd bird was a different individual, such as when both birds could be seen, or when the 2 birds sang simultaneously.

We used only complete and clear songs for analyses. We transferred these song recordings onto a computer with a sampling rate of 48 kHz and converted them into spectrograms and spectra with Canary 1.2 software (Cornell Laboratory of Ornithology, Ithaca, NY, USA). The settings were as follows: a Hamming analysis window, a filter bandwidth of 380.62 Hz, frame length of 512 points, grid resolution of 2.667 ms, overlap of 93.75%, frequency of 93.75 Hz, and Fast Fourier Transformation (FFT) size of 512 points, which had the best resolution under the maximum processing power of a Power Mac G4. All spectrograms were made at a fixed scale of 1.5 kHz/cm vs. 0.5 s/cm.

Terminology

Terms used in this paper are defined here.

Note: A continuous trace on a spectrogram. This is the basic structure of bird songs (Martin 1977, Catchpole and Slater 1995) and may appear in many shapes (Fig. 3A).

Syllable: One or several notes that always appear together in the same sequence in songs (Thompson 1970, Martin 1977, Catchpole and Slater 1995). The complexity of a syllable depends on the notes of which it is composed (Fig. 3A).

Fig. 2. A hybrid Taiwan and Mainland Hwamei captured in the Hualien area of Taiwan (left; photographer, Heng-Wei Hsu). This bird shows a shortened eye-line behind the eye in contrast to that on a Mainland Hwamei (right; photographer, Chieh-Teh Liang).

Song: A sequence of syllables uttered as a single vocalization (Baker 1996). The pause between 2 songs must be 1 s or longer (Fig. 3B).

Syllable composition: The number of notes in a syllable (Fig. 3A).

Syllable transformation: The way a syllable structure changes when a singing Hwamei switches from 1 syllable type to another.

Song initiation and termination: The 1st and final syllable types of each song, respectively.

Average number of repeated syllables per song: A standardized measurement of repeated syllables given varying song lengths. This is obtained by dividing the total number of syllables by the total number of syllable types in a song. For example, the average number of repeated syllables for the song in Fig. 3A is 18/4 = 4.5.

Syllable syntax: 2 consecutive syllable types in a song. For example, $\alpha\beta$, $\beta\gamma$, and $\gamma\delta$ are the 3 syntactic arrangements in the song of Fig. 3A.

Murmur sound: A series of muffled sounds which were impossible to separate into distinct syllables on a spectrogram.

Data processing

Following the method used in Marler and Pickert (1984), Lynch and Baker (1986), Baker (1996), and Tracy and Baker (1999), we visually inspected each spectrogram and classified all of the notes into different types according to their shapes. Notes having the same general shape were grouped into the same type (Fig. 3C). The advantage of doing this is to retain the information of similarity between variants within a type. Potential mistakes in classification (see Lynch and Baker 1993) were avoided by using a fixed spectrogram scale.

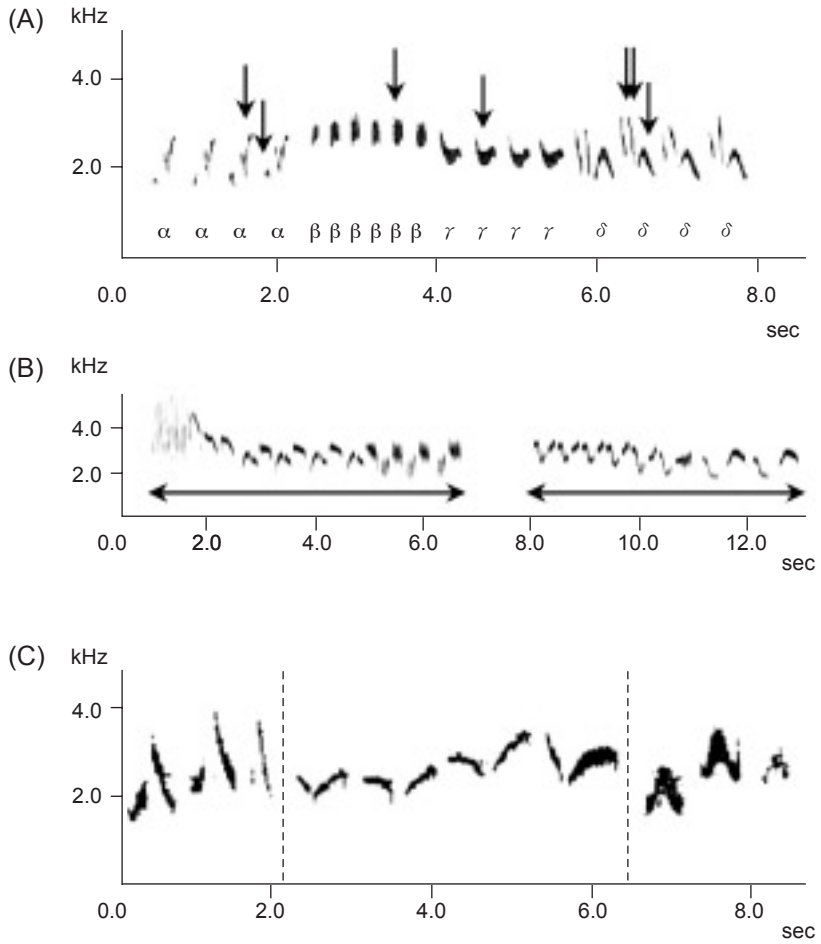

Fig. 3. (A) Examples of notes and syllables. Each arrow points to a note. There are 18 syllables in this song including 4 syllable types: α is composed of 2 notes, β and γ are composed of 1 note each, and δ is composed of 3 notes. (B) Examples of songs. The range of each arrow indicates a complete song. (C) Notes of the same general shape are grouped into the same type. Three types are shown here.

Notes were grouped into syllable types according to their patterns of occurrences.

We measured the duration, the maximum and minimum frequencies, and the frequency with the highest energy concentration for each song. To reduce potential bias caused by the different numbers of songs recorded for different birds, we used the average values of these measurements for each bird in subsequent analyses.

Sample size determination

We used the vocalization of individuals for whom we had at least 3 complete songs for analyses. To determine the number of individuals needed to represent a location, we plotted the cumulative number of syllable types found in an individual bird against the number of birds. We predetermined that the number of birds needed to represent a population must be close to the asymptotic value on the graph. For each sampling location, the accumulated syllable types of 6 individuals appeared to contain almost all of the syllable types of that location (Fig. 4). Choosing different individuals on which to perform this analysis can influence the earlier portion of the curves, but regardless of which bird was analyzed first, the final result was the same. Thus, we analyzed all the recorded songs of at least 6 birds per site, totaling 229 songs for Taiwan Hwamei (20 individuals) and 227 songs for Mainland Hwamei (20 individuals).

Data analysis

When making microgeographic comparisons, we treated songs from each recording site as a separate sample. When making macrogeographic

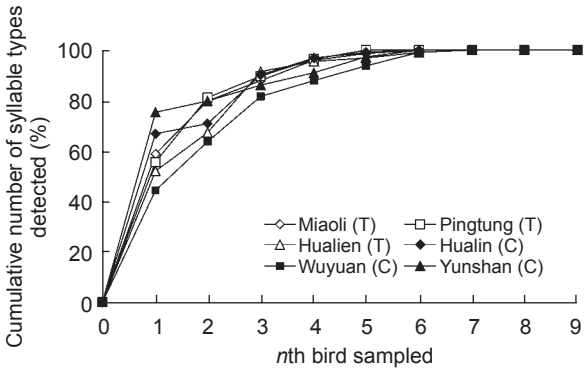

Fig. 4. Percentage of cumulative number of syllable types found in an individual plotted against the number of birds for each sample location.

Table 1. Distribution of note type, syllable type, syllable transformation, and syntax among the recording locations of Taiwan and Mainland Hwamei

Subspecies	Location	No. of songs (birds recorded)	No. of note types	No. of syllable types	No. of syllable transformation combinations	No. of syllable syntactic arrangements
Taiwan Hwamei	Miaoli	85 (7)	1	3	3	16
	Pingtung	68 (6)	0	12	1	4
	Hualien	76 (7)	2	17	0	3
	Miaoli and Hualien		1	14	1	4
	Hualien and Pingtung		0	9	0	2
	Miaoli and Pingtung		0	6	1	2
	All 3 locations		26	52	9	2
	Total for Taiwan	229 (20)	30	113	15	33
Mainland Hwamei	Hualin	84 (6)	0	21	2	12
	Yunshan	76 (7)	1	15	0	11
	Wuyuan	67 (7)	1	13	4	1
	Hualin and Yunshan		3	16	2	11
	Hualin and Wuyuan		1	12	1	2
	Yunshan and Wuyuan		0	10	0	1
	All 3 locations		27	73	11	9
	Total for Jiangxi	227 (20)	33	160	20	47

comparisons, we pooled all of the Hwamei songs from Taiwan and Mainland China into 2 respective populations.

Comparisons in this study included minimum and maximum song frequencies, the frequency of energy concentration, song duration, diversity of note or syllable types, syllable composition, patterns of syllable transformation, and syllable syntax. We also compared song initiation, song termination, and the average number of syllable repeats between locations and populations.

We compared note type, syllable type, syllable transformation, and syntax sharing between populations using the McNemar change test (Zar 1999). For continuous data, we examined differences with Student's *t*-test, analysis of variance (ANOVA), and the least significant difference (LSD).

We used a linear discriminant analysis to determine how clearly Taiwan Hwamei and Mainland Hwamei could be differentiated.

We used the computer software SAS 8.0 (Chicago, IL, USA) to perform all statistical analyses.

RESULTS

Microgeographic variation

Notes: We found 30 note types for Taiwan Hwamei, of which 86.67% were shared among the 3 locations (Table 1). Mainland Hwamei used 33 note types, of which 81.82% were shared among the 3 locations (Table 1).

Syllables: Taiwan Hwamei songs contained 113 syllable types, of which 46.02% were shared among the 3 locations. More than 10% of the syllables were each unique to Pingtung and to Hualien (Table 1), while Miaoli and Hualien shared a high proportion of syllables (70% for Miaoli, 45.16% for Hualien). Syllable compositions did not differ among the 3 locations in Taiwan ($F_{(2, 243)}$ = 1.01, $p > 0.05$) (Table 2), but the proportions of syllables shared significantly differed between Hualien and Pingtung (McNemar tests with Bonferroni correction, $p = 0.015$). Mainland Hwamei songs contained 160 syllable types, of which 45.63% were shared among the 3 locations (Table 1). More than 30% of the syllable types were unique to a location, while 23.75% of total syllable types were shared between 2 locations. Syllable compositions among the 3 locations in Jiangxi Province did not significantly differ ($F_{(2, 341)}$ = 0.02, $p > 0.05$) (Table 2); however, the proportions of shared syllables significantly differed between locations (McNemar tests with Bonferroni correction, $p = 0.015$).

A Hwamei usually repeated each syllable several times before switching to another syllable

Table 2. Syllable composition and average number of repeats per song in Taiwan Hwamei and Mainland Hwamei

Subspecies	Recording location	No. of syllable types	No. of songs	Average no. of notes/syllable[a]	Average no. of repeats/song[a]
Taiwan Hwamei	Miaoli	75	85	1.79 ± 0.87	3.62 ± 0.93
	Pingtung	79	68	1.99 ± 0.93	3.26 ± 1.27
	Hualien	92	76	1.92 ± 0.88	4.01 ± 2.60
				$F_{(2, 243)} = 1.01$, $p > 0.05$	$F_{(2, 226)} = 3.46$, $p < 0.05$
Mainland Hwamei	Hualin	122	84	2.31 ± 1.06	2.54 ± 0.76
	Yunshan	114	76	2.31 ± 1.11	2.68 ± 0.75
	Wuyuan	108	67	2.33 ± 1.17	2.41 ± 0.76
				$F_{(2, 341)} = 0.02$, $p > 0.05$	$F_{(2, 224)} = 2.32$, $p > 0.05$
Taiwan Hwamei	Taiwan	113	229	2.11 ± 0.94	3.65 ± 1.73
Mainland Hwamei	Jiangxi	160	227	2.56 ± 1.15	2.55 ± 0.76
				$t_{(266)} = 3.55$, $p < 0.001$	$t_{(314)} = 8.82$, $p < 0.0001$

[a]Data are presented as the mean ± SD.

type. Only two of the 113 syllable types (1.77%) found in Taiwan Hwamei songs were not repeated. The average number of syllable repeats per song significantly differed among locations ($F_{(2, 226)}$ = 3.46, $p < 0.05$) (Table 2), mainly because Pingtung songs had fewer syllable repeats while 1 Hualien Hwamei sang 23 syllable repeats in one of its songs. However, differences among locations remained ($F_{(2, 225)}$ = 3.69, $p < 0.05$) even when this particular Hualien Hwamei song was excluded.

In the 160 syllable types found in Mainland Hwamei songs, 9 types (5.63%) were not repeated. The average number of syllable repeats per song did not differ among sample locations ($F_{(2, 224)}$ = 2.32, $p > 0.05$) (Table 2).

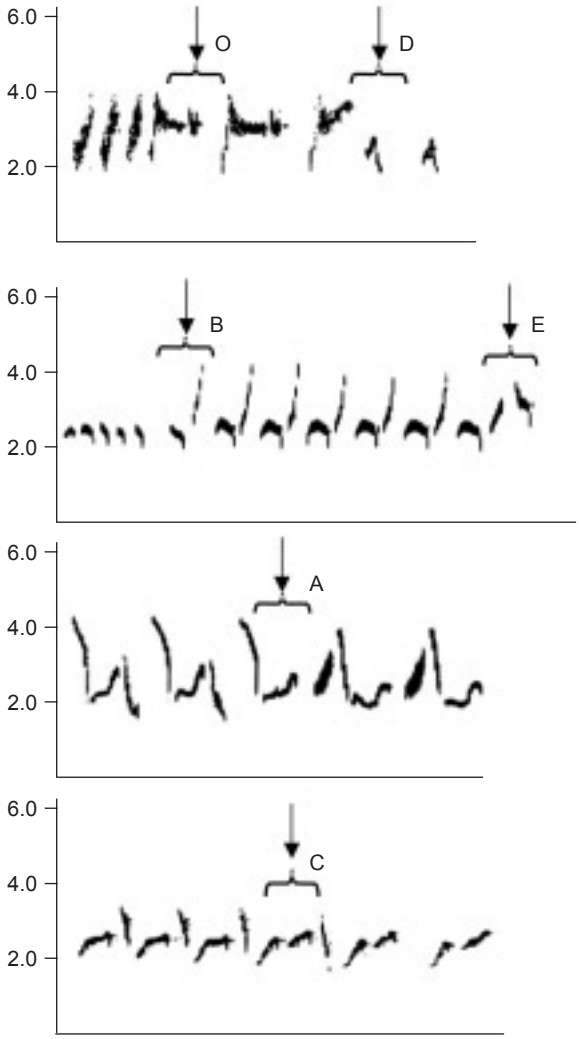

Fig. 5. Syllable transformation. There were 6 types of syllable transformation when the Hwamei switched syllables: the syllable remained the same (O), 1 note was dropped (A), the shape of the note(s) was changed (B), 1 note was added (C), 1 note was dropped and the shape of the note(s) changed (D), and 1 note was added and the shape of the note(s) changed (E).

Syllable transformation: We found 6 types of syllable transformation when Hwameis switched syllables (Fig. 5). Since each switch involved 2 syllables, there were 36 possible different combinations for a switch to take place. However, only 15 of these combinations occurred in Taiwan Hwamei songs among 1522 syllable switches in 229 songs, including 11 combinations shared between 2 or more locations (Table 1). Among these 15 combinations, OO, AO, BO, and OB occurred most frequently (See Fig. 5 for codes).

Mainland Hwamei used 20 combinations among 1869 syllable switches in 227 songs, including 14 combinations shared between 2 or more locations (Table 1). The 4 most-common types of transformation were the same as those of the Taiwan Hwamei.

Syntax and song: The syntax of Hwamei syllables was highly variable, and many arrangements occurred only once. Among the 33 syntactic arrangements that occurred more than 5 times in Taiwan, 23 occurred in only 1 location, while only 10 were shared between 2 or more locations (Table 1). In Mainland Hwamei songs, 47 syntactic arrangements occurred more than 5 times. Among these, 24 were unique to a single location, and 23 were shared between 2 or more locations (Table 1).

Hwamei songs contained greatly varying number of syllables (Taiwan Hwamei with 6~118 syllables and Mainland Hwamei with 5~92 syllables). Because the structures of songs were highly complex and variable, they were very difficult to categorize into types. We analyzed common syllable arrangements in order to detect song patterns. Out of the total 2031 syntactic arrangements, only 17 occurred more than 30 times when Taiwan and Mainland Hwameis were considered together. Based on these 17 arrangements, we found 66 three-syllable types when the subsequent syllable was included. These 66 types occurred only 107 times in Taiwan Hwamei songs and 177 times in Mainland Hwamei songs. No type occurred more than 10 times among the 229 Taiwan Hwamei songs, and only 3 types occurred between 10 and 14 times among the 227 Mainland Hwamei songs. These results show that very few individuals shared even 3 syllables in their repertoires, let alone shared their songs with others. Thus, Hwamei songs cannot be grouped into specific "types," nor can the song sequences be compared.

Measurements: The maximum and minimum

frequencies, frequency of energy concentration, and duration of Hwamei songs did not differ among locations in Taiwan ($F_{(2, 17)}$ = 2.08, 3.03, 1.33, 1.39, respectively, $p > 0.05$) or in China ($F_{(2, 17)}$ = 0.45, 0.22, 1.59, 0.77, respectively, $p > 0.05$) (Table 3).

Macrogeographic comparisons

The proportion of note types unique to Taiwan Hwamei or to Mainland Hwamei did not differ (χ^2 = 1.80, df = 1, $p > 0.05$) (Table 4), but the number of notes employed to form a syllable was significantly higher for Mainland Hwamei ($t_{(266)}$ = 3.55, $p < 0.001$) (Table 2).

Mainland Hwamei songs contained a significantly larger number of unique syllable types compared to Taiwan Hwamei songs (χ^2 = 32.97, df = 1, $p < 0.0001$) (Table 4). Among the 10 syllable types unique to Taiwan Hwamei, 5 were unique to Hualien, 4 were unique to Pingtung, and only 1 was shared among the 3 recording locations. The 57 unique syllable types in Mainland Hwamei songs occurred relatively evenly among locations: 31 in Hualin, 25 in Yunshan, and 29 in Wuyuan.

The Mainland Hwamei had significantly fewer syllable repeats compared to the Taiwan Hwamei ($t_{(314)}$ = 8.82, $p < 0.0001$) (Table 2).

Syllable transformation was more complex in Mainland Hwamei songs than in Taiwan Hwamei songs. There were 5 transformations unique to Mainland Hwamei: OD, AE, BE, CE, and CA, with most of these involving "complex" transformations (types D and E). These unique transformations occurred in all 3 sample locations in Jiangxi, China, but each occurred fewer than 3 times.

The 2 most-commonly used song initiation syllable types were the same for Taiwan and Mainland Hwamei, but the 3rd most-common initial syllable type differed. The main differences in song initiation between the 2 subspecies were the higher proportion of murmur sounds and the lower proportion of syllables containing 3 or more notes among Taiwanese birds (χ^2 = 24.44, df = 3, $p < 0.001$). The terminating syllable of both subspecies showed great variation, but the terminating syllable in Mainland Hwamei songs also contained significantly more notes than that of the Taiwan Hwamei (χ^2 = 20.56, df = 3, $p < 0.001$). Taiwan Hwamei syllables were composed of 4 notes or fewer, while 6 of the Mainland Hwamei syllables contained 5 or 6 notes. All of these more-complex syllables appeared as the terminal or penultimate syllable type.

Overall, Mainland Hwamei had greater variety and shared a larger proportion (48.94%) of syntactic arrangements between and among the 3 loca-

Table 3. Four measurements of Hwamei songs

Sub-species	Recording site	Sample size	Maximum frequency (kHz)[a]	Minimum frequency (kHz)[a]	Energy concentration (kHz)[a]	Song duration (s)[a]
Taiwan Hwamei	Miaoli	7	4.33 ± 0.29	1.44 ± 0.08	2.71 ± 0.15	11.08 ± 4.04
	Pingtung	6	4.63 ± 0.74	1.31 ± 0.11	2.75 ± 0.16	7.95 ± 3.42
	Hualien	7	4.09 ± 0.30	1.39 ± 0.09	2.85 ± 0.17	10.99 ± 3.82
$F_{(2, 17)}$			2.08	3.03	1.33	1.39
p value			> 0.05	> 0.05	> 0.05	> 0.05
Mainland Hwamei	Hualin	6	4.50 ± 0.24	1.29 ± 0.10	2.57 ± 0.15	10.40 ± 1.73
	Yunshan	7	4.57 ± 0.27	1.24 ± 0.14	2.74 ± 0.16	8.73 ± 2.15
	Wuyuan	7	4.79 ± 0.90	1.25 ± 0.20	2.71 ± 0.22	10.71 ± 4.65
$F_{(2, 17)}$			0.45	0.22	1.59	0.77
p value			> 0.05	> 0.05	> 0.05	> 0.05
Taiwan Hwamei	Taiwan	20	4.34 ± 0.50	1.38 ± 0.10	2.77 ± 0.17	10.11 ± 3.87
Mainland Hwamei	Jiangxi	20	4.63 ± 0.56	1.26 ± 0.15	2.68 ± 0.19	9.92 ± 3.15
$t_{(38)}$			1.74	3.08	1.66	0.17
p value			> 0.05	< 0.01	> 0.05	> 0.05

[a]Data are presented as the mean ± SE.

tions than did the Taiwan Hwamei, which shared only 30.30% of syntactic arrangements between and among the 3 locations (Table 1). The difference between the 2 subspecies was not statistically significant however (χ^2 = 2.78, df = 1, p > 0.05). Among syllable syntactic arrangements that occurred greater than 10 times in songs, more were unique to Mainland Hwamei than to Taiwan Hwamei (χ^2 = 11.84, df = 1, p < 0.001) (Table 4). The 2 syntactic arrangements unique to Taiwan Hwamei occurred only in Miaoli and Hualien, while 14 of the 17 syntactic arrangements unique to Mainland Hwamei occurred in all 3 locations, with the other 3 occurring at both Hualin and Yunshan.

Maximum song frequency, energy concentration, and song length did not differ between the Taiwan Hwamei and Mainland Hwamei ($t_{(38)}$ = 1.74, 1.66, 0.17, respectively, p > 0.05) (Table 3). Only the minimum frequency was lower in Mainland Hwamei songs than in Taiwan Hwamei songs ($t_{(38)}$ = 3.08, p < 0.05) (Table 3).

Linear discriminant analysis showed that the discriminant accuracy was 70.74% for Taiwan Hwamei and 77.09% for Mainland Hwamei (Fig. 6) with the variables showing significant differences between them, i.e., average number of repeated syllables per song, numbers of notes in the initiation and termination syllables, and the minimum frequency of songs.

In summary, we found no difference in Hwamei songs at the note level either micro- or macrogeographically. At the syllable level, the extent with which the 2 sites shared syllables showed a tendency to decrease with distance in China but not in Taiwan. The mean number of notes per syllable was higher in Mainland Hwamei than in Taiwan Hwamei songs. The Mainland

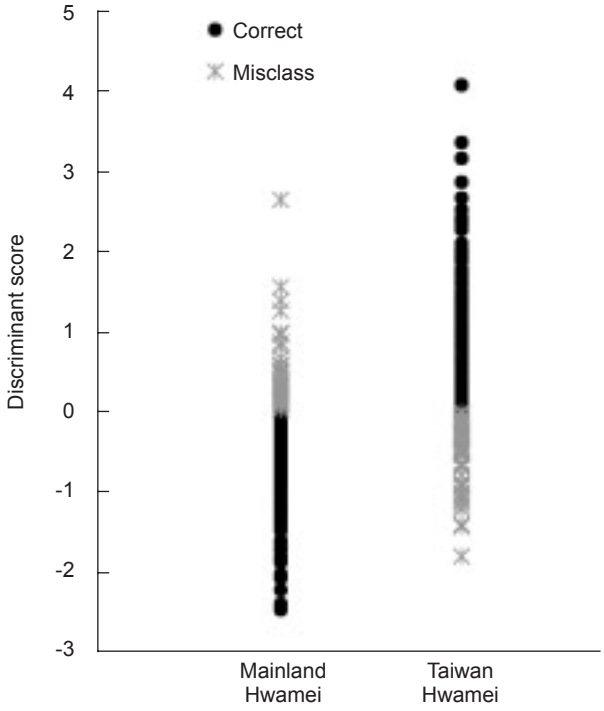

Fig. 6. Results of the discriminant analysis with average repeated syllables per song, number of notes in the initiation and termination syllables, and the minimum frequency of songs. The discriminant accuracy was 70.74% for the Taiwan Hwamei and 77.09% for the Mainland Hwamei.

Table 4. Comparisons of shared and unique note types, syllable types, syllable transformation ways, and syllable syntax

	Shared	Unique	Total	McNemar change test
Note types				
Taiwan Hwamei	29	1	30	p > 0.05
Mainland Hwamei	29	4	33	
Syllable types				
Taiwan Hwamei	103	10	113	p < 0.0001
Mainland Hwamei	103	57	160	
Syllable transformation ways				
Taiwan Hwamei	15	0	15	—[a]
Mainland Hwamei	15	5	20	
Syllable syntax				
Taiwan Hwamei	16	2	18	p < 0.001
Mainland Hwamei	16	17	33	

[a]No statistical test was performed because there were no unique transformations for Taiwan Hwamei.

Hwamei also had a greater number of unique syllable types, more combinations in syllable transformations, and fewer repeated syllables than did the Taiwan Hwamei. At the level of syntax, variations existed among Taiwan Hwamei and among Mainland Hwamei. Mainland Hwamei songs had a significantly greater number of unique syntactic arrangements than were found in Taiwan Hwamei songs. At the song level, no differences existed among all the measurements microgeographically, but the Mainland Hwamei had a lower average minimal frequency than did the Taiwan Hwamei.

DISCUSSION

Song complexity

For both the Taiwan and Mainland Hwamei, most note types were shared among the 3 sample locations, while syllables were shared less often, and most locations had some unique syllable types. Between the Taiwan and Mainland Hwamei, note types were largely the same, but Mainland Hwamei had a significantly greater number of unique syllable types, including some composed of more notes than found in Taiwan Hwamei syllables. Apparently, Mainland Hwamei used the same note types available to Taiwan Hwamei and constructed more-varied and more-complex syllables. Marler and Pickert (1984) and Van Buskirt (1997) suggested that the shape of notes is related to the phylogenetic history of the species, whereas syllables (Van Buskirk, 1997) and songs (Marler and Pickert 1984) are probably more affected by the physical and biological environment. Taiwan Hwamei and Mainland Hwamei belong to the same species, which explains why they have very similar note types. Although we did not measure habitat variables, the habitat of all tape-recording sites for this study appeared similar with dense tall shrubs and other edge vegetation. However, the acoustic environments should be much more complex for Mainland Hwamei than for Taiwan Hwamei. The Taiwan Hwamei has no sympatric congeneric species, nor is there any other bird species with similar songs in Taiwan. Five other species congeneric with the Mainland Hwamei are sympatric with the Hwamei in Jiangxi, and at least two of these are common (Yue 1996). The need to differentiate their songs from those of other species may have promoted the development of more-complex vocalizations in the Mainland Hwamei.

In addition to having more syllable types, Mainland Hwamei songs contained significantly more syntactic arrangements and significantly fewer repeated syllables per song. This means that the Mainland Hwamei switched syllable types more frequently than did the Taiwan Hwamei. The Mainland Hwamei also had more-diverse and more-complex combinations of syllable transformation than did the Taiwan Hwamei. Furthermore, both the initiating and terminating syllables of Mainland Hwamei songs contained significantly more notes than those of the Taiwan Hwamei. Most syllable types, syllable transformations, and syntactic arrangements found in Taiwan Hwamei songs were also present in Mainland Hwamei songs. These provide additional evidence that Mainland Hwamei songs have higher complexity than Taiwan Hwamei songs. Marler (1960) proposed the "loss-of-contrast" hypothesis, suggesting that the more-varied vocalizations of populations on isolated oceanic islands reflected diminished pressure for species identification, because the avifauna on such islands are relatively depauperate. This hypothesis does not apply to the case of the Hwamei, because Taiwan is a relatively large continental island connected with mainland Asia during glacial periods. This can explain why the Taiwan Hwamei does not have more-complex songs than the Mainland Hwamei but not why the songs of the Mainland Hwamei are more complex. We suggest that the avifaunal complexity of the Jiangxi area may have induced the development of more-complex acoustic signals.

Distance and topographical isolation

Learning is no doubt involved in singing by the Hwamei (Severinghaus and Tu unpubl. data) regardless of whether they have to learn to sing notes, or learn to combine notes into syllables and syllables into syntax. The final outcome of learning can be affected by the acoustic environment, by the need to differentiate species-specific sounds from competing signals, or by mistakes made during the sound-copying process (Mundinger 1982). We found differences in syllables and in syntax among locations within Taiwan and within Mainland Hwamei. In Jiangxi, Hualin and Yunshan birds shared more syllable types and syntax than either place with Wuyuan, and the distance between these 2 locations is shorter than that between either of them and Wuyuan. Many studies have shown a decline in shared vocalizations with distance (Avery and Oring 1977, Ficken and Weise 1984, Tracy and Baker 1999), because

increasing distance between locations reduces the interactions of individuals and the chance to learn from each other, and because small amounts of local mistakes made during the learning process can add up to apparent song differences with increasing distance. For Taiwan Hwamei, however, distance was probably not the strongest influence on the degree of song similarity. We found that Miaoli birds had the largest number of syntactic arrangements and the fewest number of syllable types. Hualien birds had the most syllable types and the largest average number of syllable repeats. Pingtung birds had the least variety in syntactic arrangements and the lowest average number of repeated syllables per song. The multiplicity of these differences suggests that for regions with highly rugged topography like Taiwan, the degree of isolation between locations is not necessarily proportional to distance.

Historical factors

The most-recent land bridge between Taiwan and mainland China occurred more than 10 000 years ago during the last glaciation (Ferguson 1993). The Taiwan Strait (with a minimum distance of about 90 km) has blocked all interactions between the 2 subspecies and has resulted in a substantial reduction in the similarity of their songs, but the length of isolation has not been sufficient for the 2 subspecies to develop completely different songs. The discriminant analysis showed that approximately 25% of Taiwan Hwamei and Mainland Hwamei songs could not be correctly assigned to the correct subspecies.

Two hypotheses could explain why Taiwan Hwamei songs are simpler than Mainland Hwamei songs. First, it could be a result of the founder effect. A few Mainland Hwameis who came to Taiwan via the land bridge during the glacial period were the ancestors of the Taiwan Hwamei. These "founders" only brought a portion of the vocalizations of the Mainland Hwamei, and thus Taiwan Hwamei songs were simpler than Mainland Hwamei songs. The few unique syllable types of the Taiwan Hwamei which were unevenly distributed among recording sites could very well be newly evolved communication signals that have come about through miscopying during the learning process and have not had a chance to spread through the entire Taiwan Hwamei population. Many researchers argue that founder effects will cause island populations to have fewer syllable types and simpler song structures than the continental population of the same species (Lynch and Baker 1986, Baker and Jenkins 1987, Naugler and Smith 1991, Baker 1996). Martens (1996) even claimed that when a small population first colonizes an island, it will lose part of that species' repertoire. Later the repertoire may expand again, usually by errors in learning or by invention of new song elements.

Second, the lower complexity of Taiwan Hwamei songs could have resulted from a vicariant process when the ancestral Hwamei population was divided into several smaller ones during glaciation. Hwamei songs on Taiwan might initially have been as complex as other mainland populations. The reduced interactions between refugia resulted in geographic variations of bird songs (Martens and Nazarenko 1993, Martens 1996). After glaciation, the presence of the Taiwan Strait continued to block interactions between the Taiwan Hwamei and Mainland Hwamei. Because the Taiwan Hwamei population was small relative to the Mainland Hwamei, the effect of selection and/or random drift could have resulted in the loss of some components of its vocalization. The evenly distributed syllable types of the Mainland Hwamei could be some of the features lost from Taiwan Hwamei songs.

Our results do not permit us to favor one or the other of these 2 hypotheses.

Song differentiation

Songs of the Taiwan Hwamei and Mainland Hwamei are 70% separable. The presence of hybrid Hwameis in Taiwan demonstrates that this degree of difference is insufficient to cause reproductive divergence or to lead to subsequent speciation. A similar situation was found for *Pycnonotus sinensis* and *P. taivanus*, which share a large proportion of their vocalizations and which widely hybridize where the 2 species are sympatric in Taiwan (Severinghaus et al. in press).

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