

Differences in Vocalizations of Japanese Bush Warblers on Chichijima and Hahajima in the Ogasawara Islands

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Abstract Bird songs play an important role in species recognition in reproductive behaviors. Therefore, geographic variation in the songs of a given species affects gene flow and reproductive isolation. A previous study showed that Japanese bush warblers, *Cettia diphone*, on Hahajima in the Ogasawara (Bonin) Islands sing songs with a simpler acoustic structure than those of *C. diphone* in mainland Japan. I investigated whether the acoustic structure of songs differs between the populations on two neighboring islands, Chichijima and Hahajima. In type-H songs, the maximum frequency was lower, the minimum frequency was higher, and the frequency range was, therefore, narrower on Hahajima than on Chichijima. In type-L songs, the maximum and minimum frequencies were lower and the frequency range was narrower on Hahajima than on Chichijima. A possible factor giving rise to the narrower frequency range on Hahajima is the sound transmission properties of the habitat, although further studies are needed to explore this hypothesis. Loose isolation among populations could produce differences in song structure because birdsong is a culturally transmitted trait.

Key words: acoustic structure, *Cettia diphone*, geographic variation, Japanese bush warbler, Ogasawara Islands, song

Introduction

Like morphological traits, bird songs have evolved under various selection pressures from ecological and social factors (Kroodsma and Miller, 1996). The ecological and social conditions often differ among local populations within a species, leading to geographic variation in the acoustic structure of songs (Catchpole and Slater, 1995). For example, in the blue tit, *Cyanistes caeruleus*, the proportion of songs with a trill (i.e., a series of notes repeated in sequence at a very rapid rate) is lower in closed evergreen woodland than in open deciduous woodland, probably due to the poor transmission of trills in dense vegetation (Doutrelant and Lambrechts, 2001). In addition, the proportion of blue tit songs with a trill is positively correlated with the relative density of the closely related great tit,

Parus major, within a habitat, suggesting that blue tits use species-specific songs (i.e., songs with a trill) to reduce aggressive interactions with great tits, whose songs never include trills (Doutrelant and Lambrechts, 2001). In the Japanese bush warbler, *Cettia diphone*, songs in insular populations are shorter and have fewer frequency modulations compared with those of the mainland population. Weakened sexual selection on islands, demonstrated by the lesser degree of sexual size dimorphism, may explain the simplicity of songs in insular habitats (Hamo, 2013).

Songs play an important role in species recognition in reproductive behaviors (Payne, 1986; Slabbekoorn and Smith, 2002). Birds probably use differences in acoustic structures when discriminating between heterospecific and conspecific songs. Therefore, geographic variation in song structure may disturb species recognition.

In fact, birds respond more weakly to nonlocal songs than to local songs (e.g., Nelson and Soha, 2004; Colbeck *et al.*, 2010; Dingle *et al.*, 2010; Hamao, 2016). This discrimination potentially contributes to gene flow barriers and promotes reproductive isolation (Grant and Grant, 1997; Price, 1998; see also Hamao, 2016).

In this study, I compared the acoustic characteristics of songs of Japanese bush warblers on Chichijima and Hahajima in the Ogasawara (Bonin) Islands. If the populations on the two islands are isolated, their songs might show acoustic differences that reflect the ecological and social conditions on the islands. The distance between these islands is only 36.7 km, and the Japanese wood pigeon, *Columba janthina*, can move between them (Suzuki *et al.*, 2006). However, the avifaunas of Chichijima and Hahajima are somewhat different; for example, the Bonin white-eye, *Apalopteron familiare*, inhabits only Hahajima (The Ornithological Society of Japan, 2012). Therefore, Japanese bush warbler populations on the two islands may be isolated from each other, and their songs may have diverged. Furthermore, because song structure is a culturally transmitted trait in oscine passerines (Beecher and Brenowitz, 2005), it can change rapidly relative to genetic traits (Wilkins *et al.*, 2013; see also Hamao, 2015). Thus, a comparison of song structures between Chichijima and Hahajima populations will advance our understanding of the mechanisms that produce geographic variation in bird songs.

Materials and Methods

Study sites and populations

This study was conducted on Chichijima (Chichi Island; 23.45 km²) and Hahajima (Haha Island; 19.88 km²) in the Ogasawara (Bonin) Island group. The Ogasawara Islands are subtropical oceanic islands located about 1,000 km south of Tokyo in the northwest Pacific Ocean. Vegetation on both islands consists of evergreen forests: a secondary forest dominated by tall *Schima mertensiana* and *Pinus luchuensis*, and a

dry forest of shrubby *Distylium lepidotum* and *Rhaphiolepis umbellata* (Shimizu, 1989, 2003).

The Japanese bush warbler has a wide range of distribution in the eastern Palearctic, including Japan (The Ornithological Society of Japan, 2012). An endemic subspecies, *C. d. diphone*, is resident on the Ogasawara and Iwo Islands. In *C. d. cantans*, the subspecies found on mainland Japan, males are highly polygynous and do not maintain pair bonds or undertake parental care (Hamao, 1992). In contrast, males of *C. d. diphone* guard their mates and feed their young (Hamao and Ueda, 1999; Hamao and Hayama, 2015). In comparison with the songs on Honshu, a Japanese mainland, songs on the Ogasawara Islands are acoustically simpler: each song contains fewer notes, less frequency modulation and a smaller frequency range, which is thought to be a result of weaker sexual selection pressure in insular populations (Hamao and Ueda, 2000).

Song recording

Songs were recorded from 23 males on Chichijima on 14–19 February 2016, and from 25 males on Hahajima on 19–21 February 2016. This timing may coincide with the early breeding season for *C. diphone*, as males sing very rarely during the non-breeding season (S. H., personal observation). I recorded songs at the roadside in the central part of Chichijima (along Yoake Road and at Fukiagedani; 27°03'52"–27°05'44" N, 142°12'24"–142°13'00" E; 20–270 m alt.) and in the southern part of Hahajima (between Motochi and Minamizaki; 26°37'22"–26°38'19" N, 142°09'45"–142°10'45" E; 27–116 m alt.). To avoid duplicate sampling of the same males, I walked along roads and recorded new males when I encountered them. Songs were recorded using a digital recorder (PCM-D50: Sony, Tokyo, Japan; 16-bit resolution, 44.1-kHz sample rate) equipped with a directional microphone (ECM-G5M: Sony). Songs from each singing male were recorded for at least 5 min, which was sufficient to obtain all of the individual's song types (see also Hamao and Ueda, 2000; Hamao, 2013).

Analyses

All recorded sounds were analyzed using Avisoft-SASLab Pro software version 5.2 (Avisoft Bioacoustics, Berlin, Germany). Sounds were displayed as sound spectrograms. Fast Fourier transform (FFT) lengths of 256 and 1,024 were used to produce plots for temporal and frequency measurement, respectively. The songs of Japanese bush warblers consist of an initial constant frequency (CF) part, followed by a frequency modulation (FM) part (Momose, 1999; Hamao and Ueda, 2000; Hamao, 2013; Fig. 1). Each male has several song types (Hamao, 1993; Hamao and Ueda, 2000). In a song type uttered by an individual male, the frequency of the CF part varies each time, whereas the acoustic structure of the FM part remains stable (Hamao, 1993; Momose, 1999). Therefore, I obtained six acoustic variables for the FM part of one song for each song type: maximum and minimum frequencies (Hz), frequency range (i.e., the difference between the maximum and the minimum frequencies; Hz), number of notes, length (duration; s), and number of frequency inflections [i.e., the number of changes in the sign of the derivative (slope) of the frequency on the sound spectrogram; Fig. 1].

I also recorded the number of song types of each male. Japanese bush warblers have two basic song types: H and L (Hamao, 1993; Momose, 1999). The CF part of a type-L song consists of several short whistles, whereas that of

a type-H song is one continuous whistle. Males use type-H songs in territory patrolling and type-L songs toward intruders (Momose, 2000). Because the two song types have clear differences not only in acoustic structure, but also in function, I recorded the numbers of songs that could be assigned to types H and L.

To compare acoustic variables between sites (i.e., Chichijima and Hahajima), I used generalized linear mixed models (GLMMs). The numbers of notes and frequency inflections were analyzed using a GLMM with a log link and Poisson error distribution. The maximum and minimum frequencies, frequency range, and length were analyzed using a GLMM with an identity link and Gaussian error distribution. I included the site as a fixed factor and male identity as a random factor. To compare the number of song types among males, I used generalized linear models (GLMs) with log links and Poisson error distributions. For these analyses, I made separate models of type-H and type-L songs. To test for the significance of effects, I used likelihood ratio tests. All analyses were conducted using R version 3.4.1 (R Core Team 2017) with a significance level of 0.05.

Results

The songs of Japanese bush warblers on Chichijima and Hahajima consist of CF and FM parts (Fig. 2). However, in rare cases, sounds of

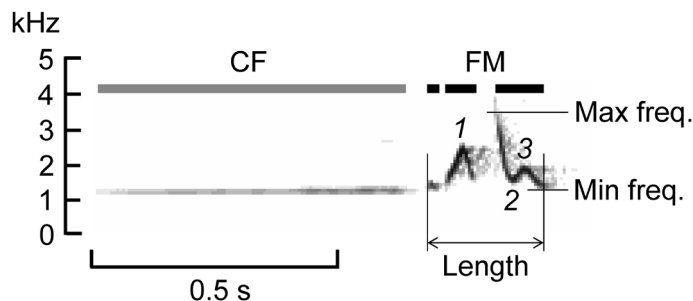


Fig. 1. Spectrogram of a Japanese bush warbler song showing the parameters analyzed. A type-H song that contains one note in the constant frequency (CF) part, and three notes and three inflections (figures in italics) in the frequency modulated (FM) part, is shown.

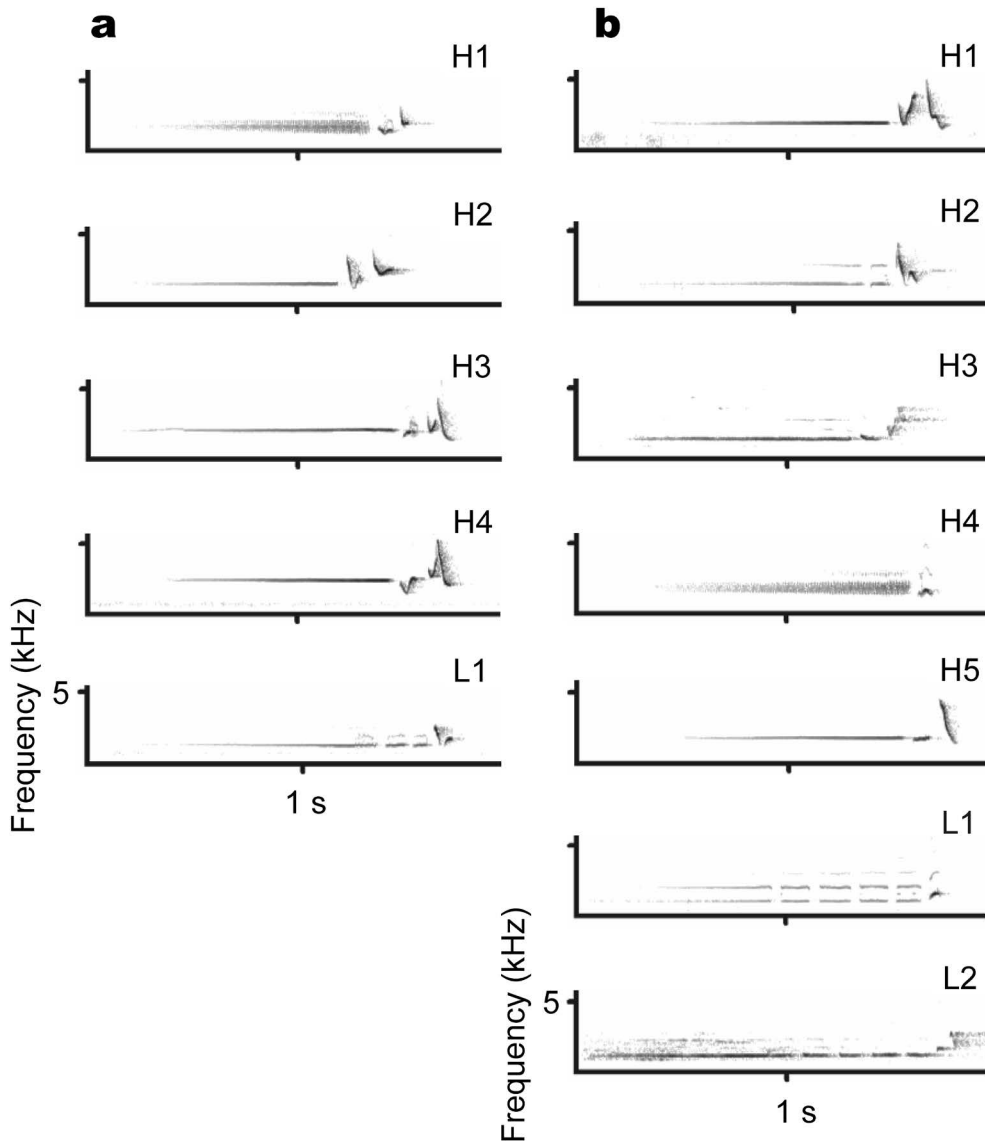


Fig. 2. Examples of sound spectrograms of Japanese bush warbler songs. Four type-H songs and one type-L song of a male on Chichijima (a) and five type-H songs and two type-L songs of a male on Hahajima (b) are shown.

only one note (at CF) were recorded. Because I could not determine whether such sounds represented a song that lacked the FM part or the CF part of a song that was interrupted, I excluded them from the analyses. Such sounds were performed by one male on Chichijima and two males on Hahajima.

I detected no significant difference between Chichijima and Hahajima in the length, number

of notes, or number of inflections in the FM parts of songs (Table 1, Fig. 3a–c). The maximum frequencies of type-H and type-L songs were lower on Hahajima than on Chichijima (Table 1, Fig. 3d). The minimum frequency on Hahajima was also lower in type-L songs, but was higher in type-H songs (Table 1, Fig. 3e). The frequency ranges of type-H and type-L songs were narrower on Hahajima than on Chichijima (Table 1,

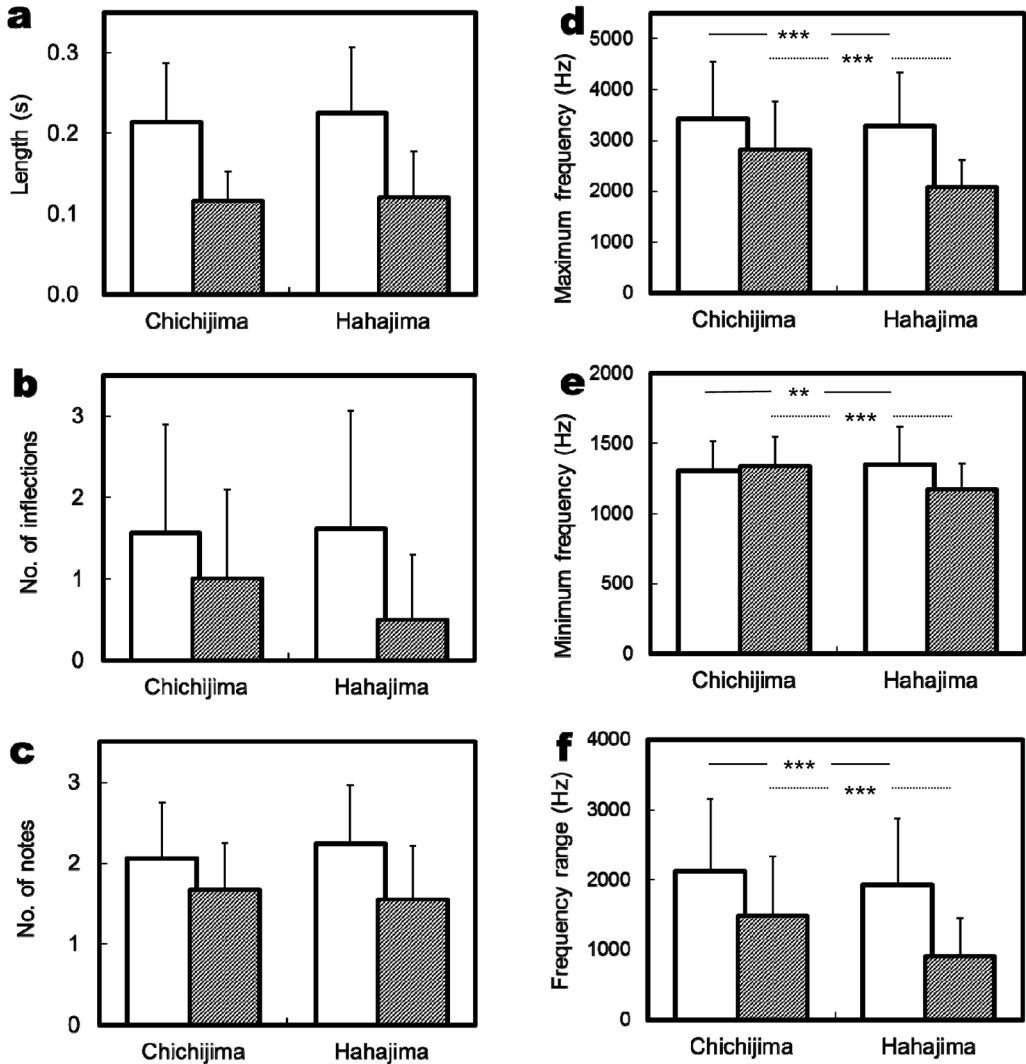


Fig. 3. Differences in the structure of Japanese bush warbler songs between Chichijima and Hahajima populations: length (a), number of inflections (b), number of notes (c), maximum frequency (d), minimum frequency (e), and frequency range (f) of the FM parts of the songs. Means + 1SD are shown. White and black bars indicate type-H and type-L songs, respectively. **: $P < 0.01$, ***: $P < 0.001$.

Fig. 3f). No difference was found in the number of song types of males for type-H or type-L songs (Table 1, Fig. 4).

Discussion

A previous study showed that the FM parts of songs of Japanese bush warblers on Hahajima have fewer notes and fewer inflections than those on Honshu (Hamao and Ueda, 2000). The sim-

pler song structure is thought to be caused by weakened sexual selection on the island (see Material and Methods section). In the present study, no difference was found in the complexity (i.e., length, number of notes, or number of inflections) of songs between Chichijima and Hahajima, which implies little difference in sexual selection pressure on the two islands. The previous study also showed that the song type repertoire is larger on Hahajima than on Honshu,

Table 1. Results of GLMM and GLM analyses of the effects of site (Chichijima and Hahajima) on acoustic variables and song repertoire, respectively, of Japanese bush warbler songs.

	Type-H songs				Type-L songs			
	Estimate [†]	S.E.	χ^2_1	<i>P</i>	Estimate [†]	S.E.	χ^2_1	<i>P</i>
Acoustic variables								
Length	0.011	0.011	-6.128	1.00	0.003	0.015	-6.531	1.00
No. of inflections	0.026	0.116	0.052	0.82	-0.663	0.435	2.260	0.133
No. of notes	0.084	0.100	0.710	0.40	-0.076	0.241	0.098	0.754
Max frequency	-156.6	158.2	12.946	<0.001	-751.4	235.0	22.071	<0.001
Min frequency	41.30	40.63	10.279	0.0013	-164.83	59.90	17.128	<0.001
Frequency range	-199.7	143.4	13.704	<0.001	-579.7	218.4	19.149	<0.001
Song repertoire								
No. of song types	0.192	0.147	1.731	0.188	-0.037	0.305	0.015	0.90

[†] Estimate relative to Chichijima.

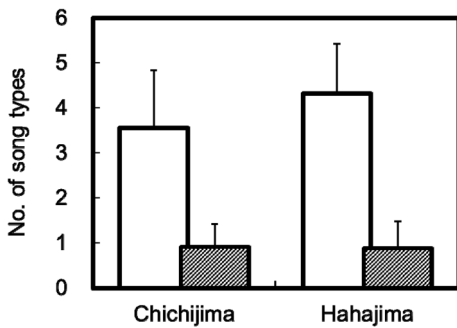


Fig. 4. Differences in the number of song types of Japanese bush warblers between Chichijima and Hahajima populations. Means + 1SD are shown. White and black bars indicate type-H and type-L songs, respectively.

which may result from the accumulation of cultural mutations due to weakened sexual selection pressure (Hamao and Ueda, 2000). In the present study, I also found that the numbers of song types did not differ between Chichijima and Hahajima. These results reinforce the conclusion that sexual selection pressure on the two islands does not differ greatly.

In comparison with the warblers on Honshu, males on Hahajima sing songs with lower maximum frequencies and higher minimum frequencies, and thus with a narrower frequency range. One possible factor contributing to the development of such song characteristics is the properties of sound transmission on the island (Hamao and Ueda, 2000). In vegetation with dense foliage, high-frequency sounds are easily attenuated

and distorted, and the songs of birds that inhabit tropical forests are restricted to a frequency range (1.5–2.5 kHz) in which sounds carry effectively (Morton, 1975). The vegetation on the Ogasawara Islands consists of evergreen forests, whereas that on the mainland is primarily deciduous forest, suggesting potential differences in the sound transmission qualities of the two habitats.

Frequency variables differed between Chichijima and Hahajima. In type-H songs, the maximum frequency was lower, the minimum frequency was higher, and the frequency range was, therefore, narrower on Hahajima than on Chichijima. In type-L songs, the maximum and minimum frequencies were lower and the frequency range was narrower on Hahajima than on Chichijima. The narrower frequency range on Hahajima may be explained by the sound transmission properties of the habitats if the forest vegetation on Hahajima is denser than that on Chichijima. Hahajima has natural mature forests, whereas shrubs growing in dry habitats are more common on Chichijima (Shimizu, 1989). However, how these differences in vegetation structure affect sound transmission is unclear. Further investigation is needed to understand the sound transmission properties of these island habitats.

I demonstrated differences in the acoustic structure of songs on two islands in close proximity to each other, using a large sample (23 males on Chichijima and 25 males on Hahajima) and appropriate statistical models (GLMMs).

The divergence of Japanese bush warbler populations on the two islands has not been investigated; no information on genetic or morphological differences between these two populations is available. However, small passerines are not likely to move frequently between the islands; the Bonin white-eye and the Oriental greenfinch, *Chloris sinica*, inhabit only some of the Ogasawara Islands (The Ornithological Society of Japan, 2012). Japanese bush warblers on Chichijima and Hahajima may be somewhat isolated from each other. Loose isolation among populations could produce song differences because birdsong is a culturally transmitted trait. The yellow bunting, *Emberiza sulphurata*, for instance, shows song differences even among populations on Honshu (Hamao *et al.*, 2018). As songs are formed through cultural learning, song differences could arise between populations on neighboring islands.

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