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ARTICLE

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Simplified song in an island population of the bush warbler *Cettia diphone*

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Abstract Song complexity and the repertoire of the bush warbler *Cettia diphone* were studied in an island and a mainland population in Japan. The song complexity (number of modulations in a song) was lower in the island population than in the mainland one. On the other hand, the repertoire size (number of song types per male) was larger on the island. Founder effect probably does not influence the island song because colonization occurred a very long time ago. Sound transmission properties of the habitat and weak selection pressure for interspecific identification might have influenced the island song, but these cannot elucidate the simpler song on the island. There is a possibility that social conditions affect song complexity in the populations; the highly polygynous mating system of the mainland population yields strong selection pressure toward complex song through acquisition of mates and/or establishment of quality territories. On the other hand, variable songs on the island seem to be affected by cultural mutation.

Key words Bush warbler, *Cettia diphone*, Island population, Mating system, Song complexity, Song repertoire

Introduction

Bird songs in island populations were found to be simpler than mainland bird songs. They have fewer syllable types and fewer song types (e.g., chaffinch, *Fringilla coelebs* [Baker and Jenkins 1987]; fox sparrow, *Passerella iliaca* [Naugler and Smith 1991]; singing honeyeater, *Meliphaga virescens* [Baker 1996]). Some researchers also reported that the structure of each song was simpler on islands than in mainland areas (Christmas Island warbler, *Acrocephalus aequinoctialis* [Milder and Schreiber 1989]; singing honeyeater [Baker 1996]). On the other hand, some studies have shown that individuals belonging to island populations sang variable songs (saddleback, *Philesturnus carunculatus* [Jenkins 1977]; Bewick's wren, *Thryomanes bewickii* [Kroosma 1985]). Several hypotheses have been offered to explain the evolution of island songs, such as the founder effect (Baker and Jenkins 1987; Naugler and Smith 1991; Baker 1996), weak selection pressure for interspecific identification (Marler 1960; see also Kroodsma 1985), and sound transmission properties (Jenkins and Baker 1984; Kroodsma 1985; Catchpole and Komdeur 1993). Although much emphasis has been given to ecological factors on islands, it is generally accepted that bird song has social functions, i.e., territorial defense and mate attraction (Searcy and Andersson 1986; Catchpole and Slater 1995). The selection pressures on bird song are dependent on the social system of the population. When considering the evolution of song on a certain island, researchers should take into account not only the ecological factors on the island but also the social factors in the population.

We investigated the songs of a small passerine, the bush warbler *Cettia diphone*, in an island and a mainland population. The song of this species is short and simple and so it is relatively easy to analyze the song structure and repertoire. Moreover, breeding ecology in the two study sites has already been investigated (see Methods). The comparison between the two populations may shed light on evolutionary causes of island bird songs. In this article, we report the differences of song structure and song repertoire of individual males between the island and the mainland population, and discuss what factors are responsible for these differences.

Methods

Study species and populations

The bush warbler has a wide range of distribution in Japan and eastern China. Five subspecies are known from Japan,

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although one of them is extinct (OSJ 1974). *Cettia diphone cantans* is the most widely distributed form in Japan and was the form studied as our mainland population. All but this subspecies are restricted to oceanic or peripheral small islands. *C. d. diphone* is endemic to the Ogasawara Islands (Bonin Islands). These oceanic islands lie about 1000 km south of Tokyo, and have been isolated since they arose in the Tertiary period.

This subspecies differs from the mainland subspecies in both morphology and ecology. The wing length of the island subspecies averaged 89% of the mainland value, while the bill length of the island subspecies is about 108% of the mainland dimension (Morioka 1977). Males on the island have smaller territories than those on the mainland, and the density of the island population is high. Some observations indicate that a smaller clutch size and male help in parental care occur on the island (Hamao and Ueda 1999). In the mainland population, males do not take any part in parental care (Hamao 1992). They acquire multiple females in succession. For example, six or seven females breeding within a male territory (Hamao 1992), and six nests, of which all were in incubation stage within a territory (Momose 1989), were reported. Potential mates are abundant because the high predation rate causes frequent remating of females.

Study area

The study was conducted on Haha-jima Island of the Ogasawara Islands and at Myoko-kogen in central Honshu, the largest island in Japan. Haha-jima Island is a subtropical, oceanic island of about 21 km^2. Average annual rainfall is 1261 mm, and mean monthly temperatures range from 17.7°C (February) to 22.9°C (August) (Japan Meteorological Agency). The island is often damaged by large typhoons. The avifauna of Haha-jima Island is impoverished. There are only eight breeding species of passerines, although the density of the four dominant species is high, i.e., the brown-eared bulbul *Hypsipetes amaurotis*, the Japanese white-eye *Zosterops japonica*, the Bonin islands white-eye *Apalopteron familiare* (formerly a honeyeater, but see Springer et al. 1995), and the bush warbler. The study area (26°38′ N, 142°10′ E) is a secondary evergreen forest on a coastal hill (20 m a.s.l.). The forest floor is dry and has little ground vegetation.

The study area on the mainland is a deciduous forest at Myoko-kogen (36°52′ N, 138°11′ E; 700 m a.s.l.) in the temperate zone. At Sekiyama (335 m a.s.l.), 6 km north of the study area, the annual rainfall is 2128 mm, and mean monthly temperatures range from −0.2°C (January) to 24.5°C (August). The maximum snow depth during the last 16 years is 3.58 m. Fifty-five species of birds were recorded during the breeding season in 1990 and 1991. The nests and/or fledglings of 21 species, of which 19 were passerines, were observed. In addition, 6 other passerine species were observed throughout the breeding season, indicating that they probably also breed there.

Analysis of songs

Song records were obtained from five males on Haha-jima Island and from eight at Myoko-kogen. The males were captured with mist nets and individually marked by a combination of colored leg rings. Songs were recorded early in the morning (between 0400 and 1000), from March 21 to April 4, 1993, on Haha-jima Island, and from June 2 to July 12, 1990, and from May 28 to July 6, 1991, in Myoko-kogen. The study period on Haha-jima Island was in the early breeding season, whereas that at Myoko-kogen took place in the middle of the breeding season. This factor does not affect the comparison between the two sites because song structure and song types do not change with season or year (Momose 1986). Each recording bout was for 7–23 min, which was sufficient to record all the song types. The repertoire size of the bush warbler is fairly small, and males sang very frequently. Individual males in Myoko-kogen had only two to five song types, and the interval between songs was short (mean ± SE, 14.7 ± 0.6 s; $n = 191$). Males did not tend to repeat the same song types. We could easily recognize the song types by listening, and the classification coincided with results of analyses by sonagrams (see also Hamao 1993).

We used a Sony TCS-2000 recorder with a built-in microphone on Haha-jima Island. In Myoko-kogen, songs were recorded using a Sony WM-D6C recorder with a Fostex M618 microphone. Additional samples were obtained from the videotapes recorded by a National AG-2400 video recorder with a National VZ-C70 video camera, which was set in front of the nests within the males territories. We analyzed the recordings on a Macintosh computer using the Sound Edit Pro. software.

Each song is composed of two portions (after Momose 1989) (Fig. 1). One has constant frequency that is emitted several times in some song types (e.g., a-5 and b-2 in Fig. 1). The following portion shows complex frequency modulations. We defined a note as a sound separated by silent intervals on a sonagram. The complexity of each song was scored by the number of modulations in notes in the modulated frequency portion. For example, as shown in Fig. 1, song type 1 of a male from Haha-jima Island has two notes in the modulated portion. These notes have one and three linear portions, respectively. Therefore, the degree of the complexity of this song is scored as 4. We also measured the highest and the lowest frequencies of each song on the sonagram. When comparing song parameters between the two sites, we calculated the average values for individual males and considered them as statistically independent data points.

Results

The lowest frequencies of songs on Haha-jima Island were higher than those at Myoko-kogen (Haha-jima Island, mean ± SE, 1.53 ± 0.06 kHz, $n = 5$; Myoko-kogen, 1.03 ± 0.03 kHz, $n = 8$; Mann–Whitney *U*-test, $U = 0$, $P < 0.01$),

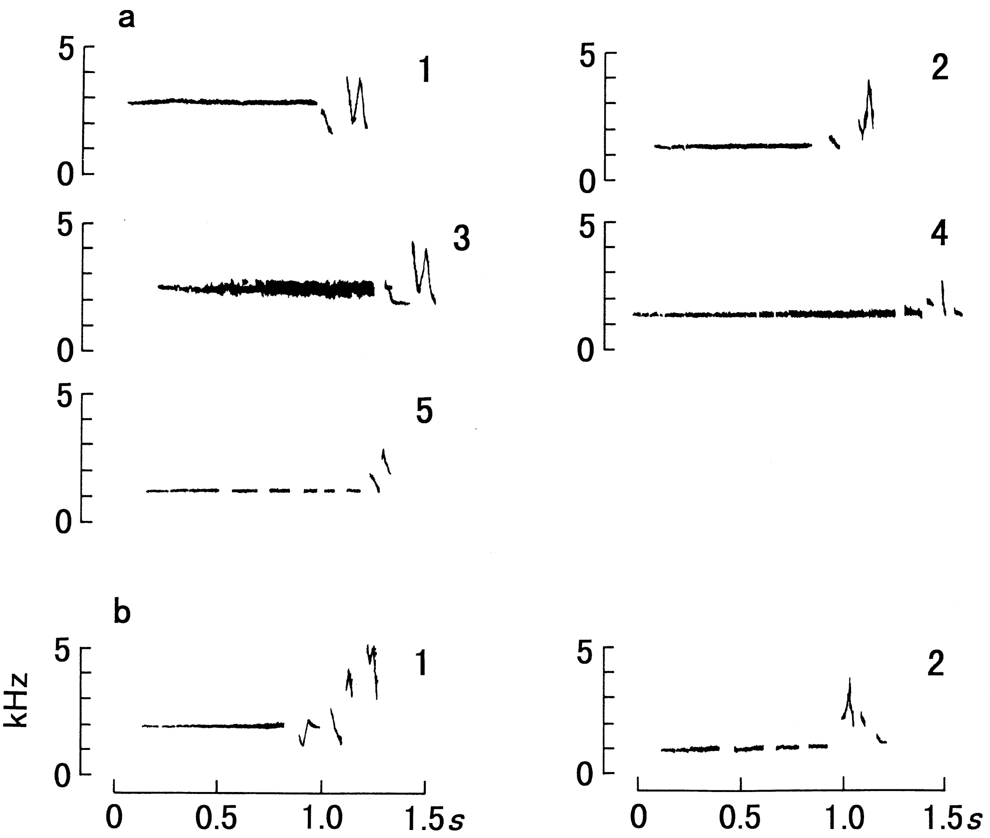

Fig. 1a,b. Sonagrams of songs in island and mainland populations of the bush warbler (*traced*) show five song types of an island male (**a**) and two of a mainland male (**b**)

Table 1. Comparison of song features between island and mainland population of the bush warbler

	Island	Mainland	Mann–Whitney U-test
Frequency range (kHz)	1.91 ± 0.09	2.91 ± 0.13	$U = 0, P < 0.01$
Notes per song	2.23 ± 0.23	2.85 ± 0.16	$U = 5.5, P < 0.05$
Complexity[a] per note	1.59 ± 0.11	2.13 ± 0.09	$U = 1, P < 0.01$
Complexity[a] per song	3.60 ± 0.51	6.17 ± 0.43	$U = 3, P < 0.05$
Song types per male	4.40 ± 0.36	2.25 ± 0.15	$U = 1, P < 0.01$

[a] Number of modulations

Figures are the average value (±SE) for five and eight males on island and mainland, respectively

but the highest frequencies were lower on Haha-jima Island (Haha-jima Island, 3.45 ± 0.07 kHz, $n = 5$; Myoko-kogen, 3.95 ± 0.12 kHz, $n = 8$; $U = 2$, $P < 0.01$). Therefore, the frequency range of songs on the island, which is the difference between the highest and the lowest frequency, was narrower than that on the mainland (Haha-jima Island, 1.91 ± 0.09 kHz, $n = 5$; Myoko-kogen, 2.91 ± 0.13 kHz, $n = 8$; $U = 0$, $P < 0.01$; Table 1).

Although the constant portion was not modulated in frequency, in the following modulated frequency portion, the number of notes and the degree of modulation varied among songs. The portion contained one to four notes in both study sites. However, the number of notes in the modulated frequency portions on Haha-jima Island was 2.23 ± 0.23 (mean ± SE, $n = 5$), whereas that at Myoko-kogen was 2.85 ± 0.16 ($n = 8$; Table 1). The difference was statistically significant (Mann–Whitney U-test, $U = 5.5$, $P < 0.05$). The complexity of notes in the modulated frequency portion was 1.59 ± 0.11 (mean ± SE, $n = 5$) and 2.13 ± 0.09 ($n = 8$), on the island and the mainland, respectively (Table 1), and differed significantly from each other ($U = 1$, $P < 0.01$). The complexity of song was also significantly higher in Myoko-kogen (Haha-jima Island, 3.60 ± 0.51, $n = 5$; Myoko-kogen, 6.17 ± 0.43, $n = 8$; $U = 3$, $P < 0.05$; Table 1).

The song types of individual males were easily identified from sonagrams (see Fig. 1). Song types were clearly separated from each other. No male sang intermediate songs between any song types. The number of song types of individual males on Haha-jima Island was 4.40 ± 0.36 (mean ± SE, $n = 5$), while that in Myoko-kogen was 2.25 ± 0.15 ($n = 8$, Table 1). The males on the island had significantly more song types than those on the mainland (Mann–Whitney U-test, $U = 1$, $P < 0.01$).

Discussion

Males of the island population of the bush warbler sang simpler songs than those of the mainland population. On the island, the number of notes per song was small, and the complexity per note was low, so the overall complexity per song was low. On the other hand, individual males on the island had more song types than those on the mainland, i.e., there was more variation at the repertoire level.

The evolution of song on islands or other isolated populations is often influenced by the founder effect (Baker and Jenkins 1987; Naugler and Smith 1991 [but see also Martin 1993]; Baker 1996). However, a population bottleneck is unlikely to increase song repertoire. Furthermore, in the case of the bush warbler, the original characteristics of the founders' songs are expected to have been lost, because the colonizing event is thought to have occurred a very long time ago. The morphology of the island subspecies differs from that of the mainland one, pointing to the long separation. In a recent phylogenetic study of the cytochrome *b* gene of the mitochondrial DNA, 0.8% of about 1000 nucleotides differ from each other between the two subspecies (M. Kajita, personal communication). This result indicates that the populations diverged about 400000 years ago, as it is known that the calibrated mutation rate of mtDNA is about 2.0% per million years in birds and mammals (Shields and Helm-Bychowski 1988).

Another hypothesis suggests that island song is influenced by the sound transmission properties of the island habitat (Jenkins and Baker 1984; Catchpole and Komdeur 1993 [but see also Dowsett-Lemaire 1994]). Morton (1975) found a tendency that forest birds used pure tonelike sounds with a restricted frequency range (1.5–2.5 kHz) in which sounds effectively carried in a tropical forest. In the case of the bush warbler, the island habitat is an evergreen forest with a dense canopy, and the songs contained less modulation; this is consistent with Morton's finding. The narrower frequency range of the island songs might have also been influenced by the sound transmission properties of the island habitat. However, the influence of forest habitat upon song structure is inconclusive. Richards and Wiley (1980) showed that less rapid modulation in songs of passerine species in North Carolina was related to the forest habitat. On the other hand, Jenkins and Baker (1984) argued that complex songs of the chaffinch in New Zealand were connected with the sound transmission properties of dense forests. It has not been clarified that forest habitat affects the simple structure of songs. Although the sound transmission properties of the island habitat might have influenced the song of the bush warbler, it is unclear that they cause simpler songs on the island.

A further hypothesis on island song is that the simpler structure and greater variation are related to weaker selection pressure for interspecific identification on islands where the avifauna is impoverished (Marler 1960; see also Miller 1982; Kroodsma 1985). One might think that this hypothesis explains the simple and variable songs in the island population of the bush warbler because only eight passerines are known to breed on the Ogasawara Islands. This hypothesis assumes that unless birds sing complex and stereotyped song in an area where there are many species, costs associated with interspecific confusion (e.g., interspecific mating) arise. However, in the case of the bush warbler, it is unlikely that the complex and stereotyped song of the mainland population has been evolved to make it prominent from other species songs because, on the mainland, there are no close relatives whose songs are similar to the song of the island population of the bush warbler. Thus, this hypothesis does not sufficiently explain how the song of the island developed, although it is not entirely ruled out.

In the evolution of island song, not only ecological factors but also social ones are important. There is a possibility that the complex songs on the mainland are influenced by the polygynous mating system. In general, mating success highly varies among males in polygynous populations. This variation may yield strong selection pressure toward complex song, which is used to acquire mates or establish quality territories, as shown in North American wrens (Troglodytidae; Kroosma 1977). Male bush warblers on the mainland are highly polygynous. Males neither undertake any parental care nor maintain pair-bonds. Moreover, duration of territories maintained is short because of the frequent replacement of territory owners (Hamao 1992). These facts suggest strong male–male competition and intensive female choice in the population. Contrary to the mainland population, in the island population, male feeding of nestlings and behavior that was probably mate guarding were observed (Hamao and Ueda 1999). Although the social system in the island population has not been entirely clarified, it appears that strong sexual selection yields complex song on the mainland, and that release from the selection pressure results in simple song on the island.

Variable songs on the island are thought to be elucidated by cultural mutation. On the island, selection pressure on various song characters may be weak. If so, when young individuals err in song learning, the next generation is imprinted to the changed songs (Martens 1996), because the cost of singing the changed song is small due to the weak selection pressure. This cultural mutation in songs could be accumulated in the population over a long time (see also Jenkins 1977; Lynch 1996). Thus, it seems that errors in song learning yield the greater song repertoire of birds on the island.

In addition, our results give some information on the capacity of memory for songs. Falls (1982) found that the degree of neighbor–stranger discrimination was inversely related to repertoire size, and suggested that birds are limited by how many variations in songs they can commit to memory. In the bush warbler, the product of song complexity and number of song types was not widely different between the two populations (Haha-jima Island, $3.60 \times 4.40 = 15.8$; Myoko-kogen, $6.17 \times 2.25 = 13.9$). From the point of view of capacity of memory for song variation, this phenomenon suggests that the fixed capacity of this species is allocated to increase song complexity on the island and to increase repertoire size on the mainland.

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