Breeding ecology of the Japanese Bush Warbler in the Ogasawara Islands

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Abstract Island and mainland populations of birds often differ in their breeding biology because of differences in ecological conditions. We studied the breeding biology of Japanese Bush Warblers Cettia diphone on Hahajima in the Ogasawara (Bonin) Islands group. Based on observations of four nesting attempts, clutches consisted of three or four eggs, which is smaller than on the mainland. Males fed the chicks, although the frequency was fairly low. Brood sizes declined during the nestling period due to starvation. Neither such male behavior nor starvation, have been reported on the main islands of Japan or on their small peripheral islands. These features of their breeding biology may have resulted from food scarcity and strong intraspecific competition on the island.

Key words Cettia diphone, Clutch size, Ogasawara Islands, Parental care, Starvation

Avian breeding biology has evolved under various ecological conditions of the habitat (Clutton-Brock 1991; Martin et al. 2000); consequently, parental behaviors within a particular species may vary among populations that are exposed to different food supplies and predator abundance (e.g. Blondel 1985; Fargallo 2004). Therefore, it is important to compare parental behaviors among local populations that have been exposed to different ecological conditions in order to understand the effects of ecological factors on breeding biology.

Islands present breeding birds with unique ecological features; for example, lack of predators and scarcity of food (Cody 1971). Small clutch size (Cody 1966, 1971), and prolonged parental care (Higuchi & Momose 1981) have been reported in insular populations, and have been discussed in relation to the ecological features on islands. Thus, it is fruitful to examine the breeding biology of a species between mainland and island populations.

The Ogasawara (Bonin) Islands are oceanic islands, situated ca. 1,000 km south of Tokyo. No species (mammalian or reptilian) predatory on birds inhabited the islands before the introduction of rats Rattus spp. and domestic cats Felis catus by human visitors (Kawakami 2002; Kawakami & Fujita 2004). Only 11 species of land birds breed on the archipelago (Shimizu 2003). These features are likely to affect the breeding ecology of birds on the islands.

Japanese Bush Warblers Cettia diphone have a polygynous mating system on the main islands of Japan (Hamao 1992). On the mainland, the warblers suffer high rates of nest predation, which results in frequent re-nesting by females. As females switch mates when re-nesting, males have abundant potential mates throughout the breeding season, which leads to polygynous mating. Males of this species provide no parental care (Haneda & Okabe 1970; Hamao 1992), and concentrate their effort on mate attraction. On the Ogasawara Islands, nest predation appears to be rare, because of the lack of native predators. If so, it is predicted that mate switching by females is infrequent, and that the availability of females for males is low. Under such conditions, males are expected to allocate effort towards parental care instead of in pursuit of polygyny. Thus, there is a possibility that the mating and parental behaviors of male Japanese Bush Warblers on the Ogasawara Islands differ from those on the mainland.
However, little information on the breeding behavior of Japanese Bush Warblers on the islands has been published, with the exception of a short report based on limited observations (Ueda et al. 1992). Here, we describe clutch size, male parental care, and various aspects of the breeding biology of Japanese Bush Warblers on the Ogasawara Islands. We also discuss the differences in the breeding biology between the island and mainland populations.

METHODS

Field surveys were carried out on Hahajima (Haha Island; 26°38′N, 142°10′E) in the Ogasawara Islands group from 9 May to 5 June 2014. Japanese Bush Warblers in this island group belong to subspecies C. d. diphone (The Ornithological Society of Japan 2012), which is genetically distinct from C. d. cantans on the mainland and small peripheral islands of Japan and from C. d. restricta on the Ryukyu Archipelago (Kajita 2002). The dominant vegetation of Hahajima is evergreen forest, but there are also many areas of cultivation.

We investigated the densities of Japanese Bush Warblers and potentially competitive species, considering competition as a possible factor affecting breeding biology. Two additional species of small insectivorous passerines, Japanese Zosterops japonicus and Bonin white-eyes Apalopteron familiaris, breed on Hahajima. Therefore, we regarded them both as potential food competitors of Japanese Bush Warblers. We made point counts at 68 points along the roads throughout the island. The average distance between nearest count points was approximately 250 m (170–290 m). We recorded the number of each of the three species seen and heard within a 50-m radius of each point in a period of five minutes between 0600 and 1630.

To investigate clutch size, and nest fate, we observed Japanese Bush Warbler nests. Nest searches were made in bamboo Pleioblastus simonii and introduced Napier grass Pennisetum purpureum thickets between 10 May and 17 May. Because of the difficulty in searching for nests in the foliage of tall dominant trees, we did not search for nests in the forest canopy. Once nests were located, they were inspected, the contents were recorded and their heights above the ground were measured. Territorial males near active nests were captured in mist nets and banded with a unique combination of colored leg rings (under license 1312171 from Kanto Region Environmental Office, Ministry of the Environment, Japan). We regarded a male singing near a nest as the owner of the territory in which the nest was located, because male bush warblers only sing within their territories (Hamao 1992; Hamao & Ueda 1999). A nesting female was also banded at one nest (nest #5). The nests were observed every day or every other day, and clutch size and nest fate were recorded.

To investigate parental behavior, and especially to establish whether males feed their offspring, we made video recordings of each nest during the nestling period. Three nests were video recorded for a total of 129.0 h (nest #1, 54.0 h over a period of 12 days [0–14 days after hatching]; nest #3, 43.8 h over 8 days [1–13 days after hatching]; and nest #5, 31.2 h over 6 days [0–8 days after hatching]). We also video recorded one young for 2.9 h on the day after it fledged from nest #6. The recordings were made mainly between 0800 and 1400.

RESULTS

In the point counts, 1.75±1.10 (mean±1SD, N=68) Japanese Bush Warblers, 3.54±3.23 Japanese White-eyes, and 1.41±1.42 Bonin White-eyes were recorded at the points.

We found five bush warbler nests in bamboo thickets (Table 1) at a mean height of 1.81 m (range: 1.42–2.42 m, N=5). One nest (#4) had already failed; a broken eggshell remained just under the nest. Another (nest #2) had been crushed, and the nesting materials (dead grasses) were damaged. Therefore, this nest was presumed to have been used in the previous year. Incubation was taking place at the other three nests (#1, #3, #5), and each contained three or four eggs. Two or three of the eggs in each clutch hatched (none or one egg failed to hatch; Table 1). Two nests (#1, #3) fledged successfully, but each nest produced only one fledgling due to a decline in the number of chicks during the nestling period. We observed (in a video recording) an uninjured dead nestling being carried away from nest #1 by one of its parents. Nest #5 fell to the ground eight days after the eggs hatched during strong winds. In addition, we found one nest (#6) at a height of ca. 6 m in the crown of a Schima wallichii tree (Table 1). We were not able to inspect the contents, but heard nestling begging calls and observed an adult bush warbler carrying food to the nest. This nest and nest #1 were located only ca. 18 m apart within the territory of the same male.
Japanese Bush Warbler in the Ogasawara Islands

Table 1. Nest site, clutch size, and the fate of Japanese Bush Warbler nests on Hahajima in 2014.

<table>
<thead>
<tr>
<th>No.</th>
<th>Location</th>
<th>Nest height (m)</th>
<th>Date¹</th>
<th>Contents</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>bamboo thicket</td>
<td>2.42</td>
<td>11 May</td>
<td>3 eggs</td>
<td>Two or three hatched on 22 May; one chick fledged on 5 June.</td>
</tr>
<tr>
<td>2</td>
<td>bamboo thicket</td>
<td>1.75</td>
<td>11 May</td>
<td>none</td>
<td>A crushed, old nest presumably used in 2013.</td>
</tr>
<tr>
<td>3</td>
<td>bamboo thicket</td>
<td>1.42</td>
<td>12 May</td>
<td>4 eggs</td>
<td>Three hatched on 22 May; one chick fledged on 4 June.</td>
</tr>
<tr>
<td>4</td>
<td>bamboo thicket</td>
<td>1.60</td>
<td>12 May</td>
<td>none</td>
<td>An eggshell was found under the nest, on a bamboo leaf.</td>
</tr>
<tr>
<td>5</td>
<td>bamboo thicket</td>
<td>1.88</td>
<td>13 May</td>
<td>3 eggs</td>
<td>Two hatched on 25 May; nest fell due to strong winds on 2 June.</td>
</tr>
<tr>
<td>6</td>
<td>Schima wallichii</td>
<td>ca. 6</td>
<td>1 June</td>
<td>nestling(s)</td>
<td>One chick fledged on 2 June.</td>
</tr>
</tbody>
</table>

¹ Date when the nest was detected.

In general, the number of species found on an island is restricted, relative to the mainland, but each species occurs at a high density (MacArthur et al. 1972; Blondel et al. 1988). The estimated density of Japanese Bush Warblers on Hahajima was five times higher than that on Kyushu, one of the main islands of Japan (Kyushu: 0.33±0.64, N=55; same methods as the present study; Shoji Hamao unpublished). The territory size of bush warblers on Hahajima is much smaller than on the mainland (Hamao & Ueda 1999), suggesting denser territory distribution, and higher density on the island. The high density suggests low food availability for individuals and strong intraspecific competition among the bush warblers on the island. Moreover, the estimated density of Japanese White-eyes was twice as high as that of Japanese Bush Warbler, while the density of Bonin White-eyes was close to that of Japanese Bush Warblers (see the Results). These sympatric insectivores appear to be competitors for food with Japanese Bush Warblers (see the Methods), thus they might also reduce the availability of food for the bush warblers.

We found that in the early stage of the incubation period the clutch consisted of three or four eggs. Ueda et al. (1992) estimated that clutch sizes of two or three eggs were normal, based on observations of nestlings and fledglings; however, this seems to have been an underestimate, because we found that the number of young in the nest declined during the nestling period. Nevertheless, the clutch size (3–4 eggs) of Japanese Bush Warblers on Hahajima appears to be smaller than that on the mainland (4–6 eggs; Haneda & Okabe 1970; Hamao 1997). A possible factor driving smaller clutch sizes is a scarcity of food (Cody 1966, 1971). On Hahajima, brood sizes declined during the nestling period (nests #1, #3, #5), and one parent bird was seen carrying away a dead chick from its nest (#1). These observations suggest that starvation occurs during the nestling stage. Starvation of nestlings has not been reported on the main-
land or small peripheral islands of Japan (Hamao 1992, 1997; Hamao & Torikai 2011). On Hahajima, food for Japanese Bush Warblers may be scarce, resulting in the reduced clutch size. Another possible factor of smaller clutches is parent birds investing more in fewer high-quality offspring, rather than in attempting to increase the number of their offspring in a given year. On Hahajima, the high density of Japanese Bush Warblers is thought to indicate strong intraspecific competition. Under such conditions, it is adaptive for parents to produce high-quality offspring with greater abilities in competition for resources (Cody 1966). Japanese Bush Warblers on Hahajima might lay smaller clutches so as to allocate greater investment in fewer individual offspring.

On Hahajima, male Japanese Bush Warblers were observed feeding their chicks, which is in contrast with other regions, where males do not provide parental care (Haneda & Okabe 1970; Hamao 1992; with one exception during which a male fed fledglings when their brief capture by humans disturbed feeding by the parents [Hamao et al. 2001]). Male feeding assistance may improve the quality and survival of the offspring, and might have evolved as a consequence of a scarcity of food and strong intraspecific competition on the island. Another possible factor steering males toward feeding is the lack of predators of their nests. On the mainland, the high pressure of nest predation results in frequent re-nesting and mate switching by females, and provides abundant potential mates for males throughout the breeding season. Thus males concentrate their efforts on mate attraction, and take no part in parental care (see the Introduction). On Hahajima, nest predation may be infrequent, because we did not find predation at least in our observation; out of four nesting attempts observed, young fledged successfully from three nests (#1, #3, #6), and one nest (#5) failed because of strong winds. Infrequent nest predation reduces the need for re-nesting by females, and thus would reduce the frequency of successive mating during the breeding season. Therefore, for males on Hahajima there may be fewer potential mates. In our observation, a male had two nests (#1, #6) in his territory, which indicates bigynous mating. Although mating patterns are not known at the population level, the low availability of females might reduce the chance of polygynous mating for males. Under such conditions, males are likely to allocate more effort to parental care rather than to mate attraction. Thus, there is a possibility that the difference in nest predation pressure between the mainland and the island affects the mating system and parental behaviors of this species.

The frequency at which males fed their offspring was lower than that of their mates, and therefore males were likely to contribute little to the growth and survival of their offspring. Males did not compensate for infrequent female feeding (Fig. 1). It is unclear why males contribute little in parental feeding.

This descriptive study indicates that there are differences in clutch size and the pattern of parental care of Japanese Bush Warblers between the populations of the Ogasawara Islands and the mainland. The study also suggests the importance of effects of food scarcity, strong intraspecific competition, low nest predation rate, and infrequent remating of females upon the parental behaviors, but these features on the island are not clearly evident. Further studies are required to understand the entire breeding system of this insular population.

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**REFERENCES**


Japanese Bush Warbler in the Ogasawara Islands


