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Authors: Kawakami, Kazuto, Harada, Sachiko, Suzuki, Tadashi, and Higuchi, Hiroyoshi

Source: Zoological Science, 25(9) : 882-887

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.25.882>

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Genetic and Morphological Differences Among Populations of the Bonin Islands White-eye in Japan

Kazuto Kawakami^{1*}, Sachiko Harada², Tadashi Suzuki²
and Hiroyoshi Higuchi³

¹Forestry and Forest Products Research Institute, Matsunosato 1, Tsukuba, Ibaraki
305-8687, Japan

²Department of Biological Sciences, Faculty of Science, Tokyo Metropolitan
University, Minami-ohsawa 1-1, Hachioji City, Tokyo 192-0397, Japan

³Laboratory of Biodiversity Science, School of Agriculture and
Life Sciences, University of Tokyo, Yayoi 1-1-1,
Bunkyo-ku, Tokyo 113-8657, Japan

The Bonin Islands White-eye, *Apalopteron familiare*, is the sole endemic avian species surviving on the Bonin Islands. The current distribution of this species is limited to only three islands of the Hahajima Island group: Hahajima, Imotojima, and Mukohjima. Imotojima and Mukohjima, which are small satellite islands of Hahajima, are about 3.6 km and 5.5 km, respectively, from the larger island. To investigate genetic and morphological differences among *A. familiare* populations on these islands, we assayed 634 bp of mitochondrial control region sequence for 132 birds from five locations among the three islands. We detected five haplotypes: two endemic haplotypes each on Hahajima and Imotojima and one on Mukohjima. Principal component analysis based on eight morphological characters of 162 birds from the three island populations revealed that birds from the small satellite islands had significantly different beak morphological characters. Our findings indicate that over-sea dispersal is rare in *A. familiare*, even when islands are separated by only a few kilometers, and suggest that little movement occurs on Hahajima. Thus, each population on each island should be conserved as an evolutionarily significant unit. The low dispersal ability of this species suggests that it is vulnerable to habitat fragmentation. Although the populations are currently stable and do not require rapid countermeasures, they should be monitored, especially those on the smaller islands.

Key words: *Apalopteron familiare*, Bonin Islands White-eye, conservation, genetic variation, morphology

INTRODUCTION

The Bonin Islands White-eye, *Apalopteron familiare*, is the sole endemic avian species surviving on the Bonin Islands, about 1000 km south of the Japanese mainland. This species, which is listed as vulnerable in the Asian Red Data Book (Birdlife International, 2001), is an omnivore, mainly forages on invertebrates, and preferentially inhabits dense forests (Kawakami and Higuchi, 2003). The population has been stable for at least the last three decades on Hahajima, the main home of this species (Kawakami and Higuchi, 2003). Although *A. familiare* had been placed in the Meliphagidae (Deignan, 1958), a study of 12S rRNA sequences by Springer et al. (1995) showed that it is a member of the white-eye family Zosteropidae.

The Bonin Islands are subtropical oceanic islands located within 26°32'–27°43'N and 142°05'–142°14'E in the

northwestern Pacific Ocean. They consist of three main island groups (Mukojima, Chichijima, and Hahajima). The islands are primarily volcanic, dating to the Tertiary (Kuroda et al., 1981).

The islands were first colonized by western and Polynesian groups in 1830 (Tsuji, 1995). These immigrants exploited the forests, established crops such as sugarcane, corn, and sweet potatoes, and introduced domestic animals such as pigs, goats, cows, ducks, chickens, cats, and rats, all of which eventually became feral (Tsuji, 1995). The Bonin Islands became a Japanese territory in 1876, and deforestation and animal introductions accelerated. On the main islands of Hahajima and Chichijima, all areas amenable to cultivation were converted to sugarcane fields, until the value of this crop suddenly dropped in 1910 (Kurata, 1983). The Japanese government forced almost all inhabitants to evacuate the Bonin Islands in 1944 (Funakoshi, 1992). After World War II (WWII), the islands were under American occupation until their return to Japan in 1968 (Kurata, 1983). Subsequently, only Chichijima and Hahajima were recolonized by civilians and the other islands remained uninhabited.

* Corresponding author. Phone: +81-29-829-8257;
Fax : +81-29-873-1543;
E-mail: kazzto@ffpri.affrc.go.jp

doi:10.2108/zsj.25.882

Of the two subspecies of *A. familiare*, the nominate form *A. f. familiare* occurred at least on Mukojima and Nakodajima of the Mukojima group, and Chichijima (Moriyama, 1930; Suzuki, 2003, 2004; Suzuki and Morioka, 2005). On these islands, there has been no evidential record of *A. familiare* since 1930 (Yamashina, 1930). Although the reason for its disappearance is not clear, feral goats caused intensive habitat loss on these islands (Shimizu, 1993), and almost all forests have been changed to grasslands or been denuded (Shimizu, 1993). On Chichijima, *A. f. familiare* has not been observed since 1829, other than a report of a small number in the 1970s, which are thought to have escaped from captivity (Morioka and Sakane, 1978). Since a large number of feral cats already lived on Chichijima in 1853 (Jones, 1856), predation likely caused the population decline of *A. f. familiare*. This subspecies is considered extinct (Ministry of the Environment, 2002).

The other subspecies, *A. f. hahasima*, currently exists on the three islands of Hahajima, Mukohjima, and Imotojima of the Hahajima group (Suzuki, 1991) (Fig. 1). Although this subspecies also occurred on Meijima in this island group, it disappeared between 1904 and 1925 (Moriyama, 1930). There is no record of *A. f. hahasima* on Hirashima or Anejima, the other satellite islands of the Hahajima group, except for one observation each in 1976 and 1978, respectively (Morioka and Sakane, 1978).

The distribution of islands in the Hahajima group with and without *A. familiare* is unbalanced, in that the Bonin

Islands White-eye occurs alternately on islands. A population has not reestablished on Meijima, even though it is less than 1 km from Imotojima. The introduced Japanese White-eye, *Zosterops japonicus*, whose niche is similar to that of the native white-eye, exists on those islands lacking the native white-eye (Suzuki, 1991; Kawakami and Higuchi, 2003). Thus, these islands are likely also suitable for the Bonin Islands White-eye. However, the relationships between populations of the native white-eyes on different islands have never been investigated. The purpose of this study was to clarify the inter-population relationships of Bonin Islands White-eyes based on genetic and morphological analyses.

MATERIALS AND METHODS

Study sites

Field surveys were conducted on Hahajima, Mukohjima, and Imotojima (Fig. 1). These islands are 20.2, 1.4, and 1.2 km² in size, respectively. The monthly mean temperature is about 18–28°C, with an annual mean temperature of about 23°C (Japan Meteorological Agency, 2001). Monthly precipitation is 60–170 mm, with an annual precipitation of about 1300 mm (Japan Meteorological Agency, 2001). About 400 people inhabit Hahajima, which is mostly covered with secondary forests established on what was previously agricultural land. The forests are dominated by *Ardisia sieboldii*, *Machilus boninensis*, *Rhaphiolepis wrightiana*, and *Schima mertensiana*, with tree layers 5–15 m high. Mukohjima is an uninhabited island whose only inhabitants were troops during WWII (Ohzeki, 1995). The vegetation is mainly *Planchonella obovata* var. *dubia* and *Wikstroemia pseudoretusa*. Imotojima was inhabited by at most about 30 people during the 1890s to 1920s (Tsuji, 1995) and is mainly covered by *W. pseudoretusa* and *R. wrightiana*. Three, one, and one survey sites were respectively located on the three islands: KTK, SKM, and TMG on Hahajima; MKH on Mukohjima; and IMT on Imotojima (Fig. 1).

Genetic analysis

We obtained blood samples from birds caught in mist nets at each site in June or July 2003, 2004, and 2005. To prevent re-sampling, captured individuals were marked with metal rings. We assayed 29, 27, 28, 34, and 14 samples collected at KTK, SKM, TMG, MKH, and IMT, respectively. Samples were preserved in 99% ethanol.

Total DNA was isolated by using silica gel, according to the procedures of Boom et al. (1990). We amplified a portion of the mitochondrial DNA (mtDNA) control region, including domain III, using PCR. We used the following set of primers: forward 5'-GAGAACCGAGCTACTCAAC-3' and reverse 5'-CGTGTGGATTG-TATTTT-3'. All PCR reactions were performed in 10- μ l reaction mixtures containing 1 μ l of dNTPs (2.5 mM, TaKaRa, Shiga, Japan), 0.1 μ l of Taq polymerase (5 units/ μ l; TaKaRa), 5.5 μ l of distilled water, 1 μ l of 10 \times PCR buffer (TaKaRa), 0.2 μ l of each primer (10 pmol/ μ l), and 2 μ l of DNA solution. The thermal profile comprised an initial denaturing step at 94°C for 90 sec; 30 cycles of 95°C for 15 sec, 54°C for 30 sec, and 72°C for 50 sec; and a final extension step at 72°C for 7 min. The resulting products were purified by using Microcon-100 (Millipore, Billerica, MA, USA), sequenced with a Big Dye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) according to the standard protocol, and visualized on an ABI PRISM 377 DNA sequencer (Applied Biosystems).

Morphological analysis

Bonin Islands White-eyes were captured with mist nets at the five survey sites to compare morphological characters among survey sites in June or July 2002, 2004, 2005, and 2006. We analyzed

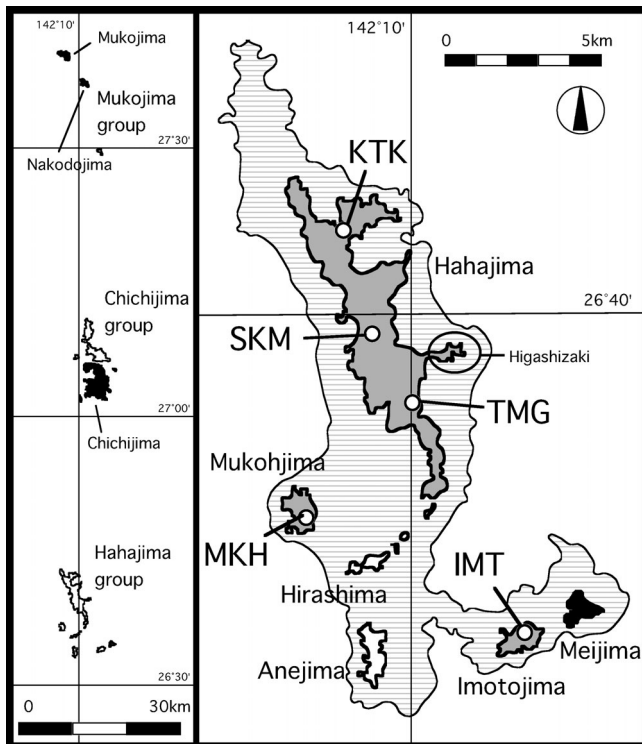


Fig 1. Bonin Islands (left) and the Hahajima group (right). Open circles indicate survey sites. Horizontal hatching indicates water depth <100 m. White and gray islands in the right-hand map indicate the absence and presence of Bonin Islands White-eyes, respectively. White-eyes went extinct on the black islands after 1830.

Table 1. Haplotypes of the 634-bp D-loop region for Bonin Islands White-eyes, and the haplotype composition of each population. Dashes indicate identity with the base in haplotype H1. Haplotype diversity was calculated by the formula $n(1-\sum x_i^2)/(n-1)$, where n is the sample size, x_i is the frequency of each haplotype.

Haplotype	Nucleotide position				Hahajima				Mukohjima	Imotojima	Total
	198	199	272	421	KTK	SKM	TMG	Subtotal	MKH	IMT	
H1	T	T	G	A	28	23	23	74			74
H2	–	–	A	–		4	5	9			9
M1	–	C	–	–	1			1	34	1	36
I1	C	–	–	–						4	4
I2	C	–	–	G						9	9
Total					29	27	28	84	34	14	132
Haplotype diversity					0.069	0.262	0.304	0.215	0	0.538	0.606

–: the same as Haplotype H1.

16, 54, 25, 27, and 40 individuals collected at KTK, SKM, TMG, MKH, and IMT, respectively. The captured individuals were marked with metal rings to prevent repeated sampling of the same individuals. All captured individuals were measured with digital calipers and a digital scale. The following measurements were taken: natural wing length, tail length, tarsus length, beak length (from the base to the tip of the upper mandible), beak height and width (at the posterior nostril), total head length, and body weight. The birds were weighed after being held in non-airtight paper bags for at least 5 min to standardize weight by evacuation. Throughout the study, the same researcher measured birds to avoid possible inter-observer variation. Only measurements of adults were used for the following analysis, because it is likely that juvenile morphology differs from adult morphology. The sexual dimorphism of this species is unknown. As the birds were randomly captured with mist nets by the same method at all sites, the sex ratio was estimated to be roughly similar among sites. To support this assumption, we identified gender, using cloacal shape, when possible, but because the surveys were not conducted during the peak breeding season, the number of gender-identified individuals was limited. We also tested sex-ratio differences among the survey sites. We conducted a principal component analysis (PCA) and plotted birds from each survey site in the morphological space defined by the first two principal components.

RESULTS

Genetic analysis

We obtained a 634-bp sequence for each of 132 individuals. Of the 634 bp, four sites (0.6%) were variable, and all four involved transitions. These sites defined five distinct haplotypes (H1, H2, M1, I1, and I2; Table 1). M1 was found on all three islands and was the only haplotype found on Mukohjima. In addition to M1, two endemic haplotypes (H1 and H2) were detected on Hahajima. H1 was dominant at all three sites on Hahajima, H2 did not appear at KTK, and M1 was not present at the other two sites. The haplotype composition was not significantly different between SKM and TMG (Fisher's exact test, $P=0.52422$), whereas it absolutely differed between KTK and the other two sites. On Imotojima, two endemic haplotypes (I1 and I2) and M1 were detected. Haplotype diversity was highest on Imotojima and was 0.606 over all survey sites. The sequence of H1 was deposited in the DDBJ nucleotide data bank (accession no. AB436812).

Morphological analysis

The sex ratio (male:female) of identified individuals was 5:3 at KTK, 16:11 at SKM, 5:7 at TMG, 5:4 at MKH, and 19:20 at IMT. The ratio did not significantly differ among

Table 2. Factor loadings of the eight morphological measurements on axes PC-I and PC-II. Bold type indicates the three largest loadings for each principal component.

	PC I	PC II
Wing length	0.5080	0.1096
Tail length	0.3676	0.2059
Tarsus	0.2957	0.1505
Beak length	0.3971	–0.3773
Beak height	0.1233	0.5831
Beak width	0.0163	0.6377
Total head length	0.5428	–0.1723
Weight	0.2273	–0.0655
Eigenvalues	2.43	2.06
Cumulative proportion of total variance	30.36	56.07

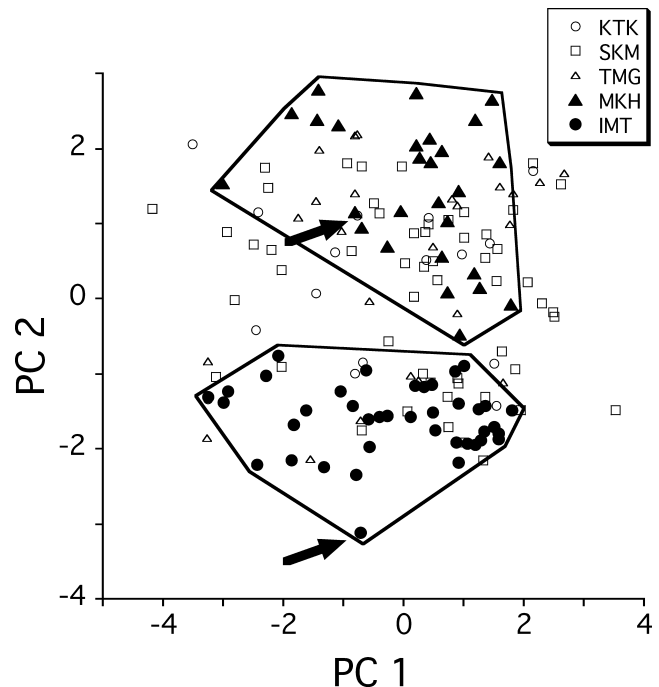


Fig 2. Morphological positions of individuals from the five survey sites relative to PC-I and PC-II. Black arrows indicate M1 haplotype individuals collected at the IMT and KTK survey sites (see Fig. 1).

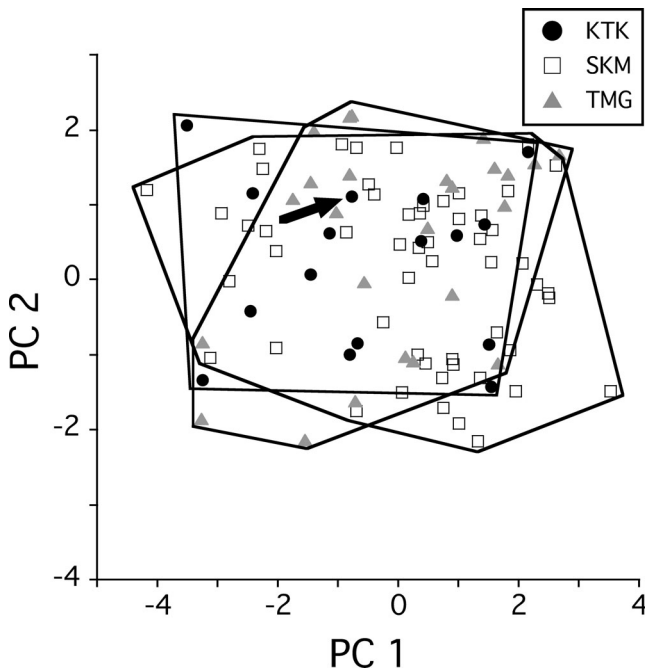


Fig 3. Morphological overlap of individuals from the three survey sites on Hahajima (see Fig. 1).

sites ($\chi^2=1.637$, $df=4$, $P=0.80$).

The ordination of the eight morphological variables by PCA yielded two axes that accounted for 56% of the variance in the data set (Table 2). The first principal component (PC-I), which accounted for 30.4% of the variance, represented body size. PC-II, which accounted for 25.7% of the variance, represented beak characteristics.

The distribution of individuals in morphological space showed that body size mostly overlapped at all survey sites (Fig. 2). However, the populations on the two satellite islands, Mukohjima and Imotojima, were separated along the PC-II axis (Fig. 2). The former population has thicker and shorter beaks than the latter. Although the slopes were not significantly different between the two groups ($P>0.05$), there was a significant difference in intercept among groups (ANCOVA; $F_{2,89}=341.282$, $P<0.0001$). The individuals from the three localities on Hahajima widely overlapped in morphological space (Fig. 3), showing morphological similarity among the survey sites (MANOVA: Wilks' $\lambda=0.953$, $F_{4,182}=1.115$, $P=0.351$). The individual with haplotype M1 at KTK was within the morphological range of the Mukohjima population, which had only M1 individuals, whereas the M1 individual from IMT was isolated (Fig. 2).

DISCUSSION

Geographic isolation of white-eyes

The results of our genetic analysis indicate that gene flow among the three populations is restricted. As the distances from Hahajima to Mukohjima and Imotojima are about 3.6 and 5.5 km, respectively, we infer that the restricted gene flow results from oceanic isolation. Thus, over-sea dispersal is rare in *A. familiare*, even when islands are separated by only a few kilometers. A population has not reestablished on Meijima, likely due to this over-sea dis-

persal barrier. This finding may reflect only limited female dispersal, as the assay was conducted with mtDNA. However, the fact that there have been few *A. familiare* sightings on Hirashima and Anejima suggests that both males and females infrequently migrate over the sea. One individual with the Mukohjima haplotype was found on each of Imotojima and Hahajima. The morphology of the Imotojima individual was not within the range of Mukohjima individuals, whereas the individual on Hahajima was within that range. This result implies that at least the former was not a temporal visitor from Mukohjima.

In addition to the lack of movement between islands, this species seems to seldom move about on Hahajima. Although the distance between KTK and SKM was only about 3.5 km, gene flow was restricted. This difference in haplotype composition among sites on Hahajima might be due to past habitat fragmentation. Hahajima had vast sugarcane cultivation, and the forested area declined in the early 1900s. The forest patch near KTK was almost completely separated from the forest that includes SKM and TMG in the early 1900s (Katahira, 1982), and the Bonin Islands White-eye prefers dense forests (Kawakami and Higuchi, 2003). The land cultivated before WWII was abandoned and developed into secondary forests (Okutomi et al., 1983; Yoshida and Oka, 2000). Although the forests near KTK and SKM are currently connected by secondary forest, not enough time has passed since the forests were reconnected for the fragmented populations to intermingle. The mobility of the white-eye is restricted even within an island. Higashizaki is in the easternmost part of Hahajima, connected to the middle of the island by a 150 m wide corridor of small bushes, grasslands, and bare ground (Fig. 1). There are no Bonin Islands White-eyes in the isolated Higashizaki forest, although introduced Japanese White-eyes occur there (Hayato Chiba, pers. com.). These observations suggest that open habitats, as well as water, can be a dispersal barrier for the Bonin Islands White-eye. Although a low frequency of over-sea dispersal has been indicated for the Australian White-eye, *Z. lateralis*, and the Seychelles Grey White-eye, *Z. modestus* (Degnan and Moritz, 1992; Degnan, 1993; Rocamora and Richardson, 2003), this is the first time such restricted migration between such close islands has been detected in white-eyes.

Only a few haplotypes were detected on Hahajima, and the genetic diversity of the population was lower than that of the Imotojima population, likely because of past habitat loss. About 60% of the forest area on Hahajima was cultivated before WWII (calculation based on Katahira, 1982). This population possibly suffered a serious bottleneck. However, as our results were based on a limited mtDNA region, additional loci must be assayed to adequately assess the genetic diversity of each population.

Only one haplotype was detected on Mukohjima, whereas three were found on Imotojima, although the two islands are similar in size. A strong bottleneck likely caused this lack of haplotype diversity on Mukohjima. However, we cannot reject the possibility that the uniform haplotype was due to sampling error caused by low-frequency haplotypes. Further analysis with additional individuals is needed.

The sea level at the last glacial maximum about 20,000 years ago was ca. 100 m lower than it is today (Siddall et

al., 2003), and the Hahajima group islands are thought to have been connected at that time (Kaizuka et al., 2000). Fig. 1 shows the water depth <100 m surrounding the island group and demonstrates how the islands were likely connected in the past. Possibly, only one population existed at that time. The wide distribution of haplotype M1 may be due to incomplete lineage sorting that originated before the islands separated, as well as recent dispersal. Another possibility is that the distribution of this haplotype was caused by homoplasy. Assaying a longer sequence may help to identify the cause.

The morphological variation in the Mukohjima and Imotojima populations also suggests infrequent migration from one to the other due to the sea barrier. The ranges of morphological traits in the two satellite insular populations were within the variance of the Hahajima population. We detected a difference in beak shape, which can change rapidly due to dietary variation (Pimm, 1988; Grant and Grant, 2002; Amiot et al., 2007). Differences in food items among populations should be investigated in future surveys.

Conservation implications

Our results indicate that the populations on each island are independent from others. Each population on each island should be conserved as an evolutionarily significant unit. This finding highlights the importance of conserving the smaller populations on the satellite islands. Such small populations are more vulnerable to stochastic events, and they cannot be complemented by individuals from other populations because of the possibility of genetic contamination (Frankham et al., 2002). The genetic diversity of the entire Hahajima group population is not low, compared to other threatened species (cf. Koike and Matsui, 2003). However, no population is particularly genetically diverse, especially on Mukohjima. The lack of genetic diversity implies that these populations are vulnerable to disease, pollution, climate change, and other environmental changes (Allendorf and Leary, 1986; Lande, 1999).

As Imotojima and Mukohjima are uninhabited, populations there are less threatened than those on Hahajima. One threat to Bonin Islands birds is introduced terrestrial predators, such as feral cats (Kawakami, 2000; Kawakami and Higuchi, 2002). Although feral cats have been observed on Mukohjima (Kawakami, 2002), none have been seen recently. Predation by introduced rats also leads to declines in insular bird populations (Atkinson, 1985), and the black rat, *Rattus rattus*, occurs on almost all of the Bonin Islands (Kawakami, 2008). However, there has been no record of rat predation on land birds there. Another concern is potential competition from introduced white-eyes (Morioka and Sakane, 1978). However, no negative impacts on the native white-eye population have been identified (Kawakami and Higuchi, 2003), although competitive effects on native bird populations have been suggested in the Hawaiian Islands (Mountainspring and Scott, 1985). The deserted islands show no human impacts. However, these island environments are not unchanged. About 20% of the forest on Imotojima is secondary. The structure of secondary forests is thought to be relatively poor and less resistant to inclement weather than that of primary forests. Furthermore, the Bonin Islands have become drier than in the past; one cause is

recent global warming (Oka et al., 2000). The water supply is low on the small Bonin Islands (Kawakami, 2006). Such factors can threaten small populations on satellite islands. Although countermeasures need not be rapidly implemented, the populations on these islands should be carefully monitored.

Hahajima is widely covered by forests, and Bonin Islands White-eyes occur everywhere (Kawakami and Higuchi, 2003). The population density of the white-eye has been stable since the 1970s (Kawakami and Higuchi, 2003), and the population is not seriously threatened at present. However, the low dispersal ability of this species suggests that it is vulnerable to habitat fragmentation. Deforestation has occurred since the return of the islands to Japanese possession (Kawakami and Higuchi, 2003). If deforestation continues, the white-eye population could decline significantly.

ACKNOWLEDGMENTS

We are grateful to Masaki Fujita, Emi Sunaga, Minako Murakami, Nanami Kawamura, Yutaka Yamamoto, Kazuhiko Uemura, Hiroki Umeno, and Reina Tazawa for field assistance; Mamoru Kikuchi and Isamu Matsunaga for transportation; Ryoko Segawa for her support for the genetic analysis; and Seiji and Keiko Tazawa for accommodation. We also thank anonymous reviewers for their helpful comments. This study was partly supported by the Global Environment Research Fund of the Ministry of the Environment of Japan (F-051).

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(Received February 29, 2008 / Accepted June 6, 2008)