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RESEARCH ARTICLE

Inferring the ancient population structure of the vulnerable albatross *Phoebastria albatrus*, combining ancient DNA, stable isotope, and morphometric analyses of archaeological samples

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Abstract The history of population structure is a key to effective wildlife management and conservation. However, inferring the history of population structure using present genetic structures is problematic when the method is applied to species that have experienced severe population bottlenecks. Ancient DNA analysis seemed to be a promising, direct method for inferring ancient population structures. However, the usual methods for inferring modern population structure, i.e. the phylogeographic approach using mitochondrial DNA and the Bayesian approach using microsatellite DNA, are often unsuitable for ancient samples. In this study, we combined ancient DNA obtained from zooarchaeological bones with carbon/nitrogen stable isotope ratios and morphological variations to infer ancient population structure of the short-tailed albatross *Phoebastria albatrus*. The results showed that the bird existed in two populations, between which the genetic distance was greater than that of distinct sister albatross species, although no subspecies of *P. albatrus* have been proposed. Our results suggest that the birds at the present two breeding regions (Torishima in the Izu Islands and two islets of the Senkaku Islands) are descended from these two ancient populations, and that reevaluation of the status and conservation strategy for the species is required. Our results also indicate that lineage breeding on the Senkaku Islands has drastically reduced genetic diversity, while that on Torishima has not. The approach proposed in this study would be useful for inferring ancient population structure, using samples of highly mobile animals and/or samples from archaeological sites, and the reconstructed ancient population structure would be useful for conservation and management recommendations.

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Introduction

Because all evolutionary forces, such as natural selection, genetic drift, mutation, and gene flow, are ultimately related to population structure, the history of population structure is an important element in understanding evolution (Avise 2000; Fox et al. 2001; Futuyma 1986). Present population structures are usually inferred by analysing genetic structure, i.e. the distribution patterns of neutral molecular markers among breeding sites (Avise 2000). Maternally inherited mitochondrial DNA (mtDNA) and bisexually inherited microsatellite DNA are two of the molecular markers most widely used for this purpose, because of their fast mutation rates. Present genetic structures reflect both ongoing and past gene flow (Avise 2000; Avise et al. 1987; Templeton et al. 1995). Avise et al. (1987) argued that the history of population structure can be reconstructed from the current genetic structure by assuming that genetic drift has fixed different alleles among isolated populations. The history of population structure in many organisms has been estimated from this phylogeographic perspective and used in wildlife management and conservation.

However, inferring the history of population structure using present genetic structures is problematic when the method is applied to reconstruct the population histories of species that have experienced severe population bottlenecks. This is because allele frequencies may have been influenced by genetic drift and historical information on the population structure can be lost (Crandall et al. 2000; Excoffier and Schneider 1999; Knowles and Maddison 2002; Templeton and Georgiadis 1995). For example, Crandall et al. (2000) found that two recently divided small (e.g. bottlenecked) populations could be regarded as two long-term isolated populations, if divergent alleles in an ancestral population were fixed by genetic drift that has a more pronounced effect in small populations than in large ones. They suggested that in such the case, to manage the "two small populations" as different management units would result in decreased genetic diversity and increased risk of inbreeding depression (Crandall et al. 2000).

Ancient DNA, which is DNA extracted from historical, paleontological, and archaeological remains, has recently been applied to wildlife conservation (Leonard 2008; Ramakrishnan and Hadly 2009). Ancient DNA analysis is a promising, direct method for inferring ancient population structures, which can be studied using resident animals or animal bones that have accumulated within colonies (Hadly et al. 1998, 1995; Lawrence et al. 2008). However, the usual methods for inferring modern population structure, i.e. the phylogeographic approach using mtDNA (Avise 2000) and the Bayesian approach using microsatellite DNA, or STRUCTURE analysis (Pritchard et al. 2000; Rosenberg et al. 2002), are often unsuitable for ancient samples. The phylogeographic approach requires information on the breeding site for each sample. However, knowing where the animals bred is impossible for samples of mobile animals and samples from archaeological material. STRUCTURE analysis for inferring the ancient population structure is an impractical solution for this problem, because low numbers of nuclear DNA copies remain in typical ancient samples and nuclear DNA analysis is difficult. For example, Ramakrishnan & Hadly (2009) reviewed ancient-DNA studies that investigated population-level genetic variation, only two of which dealt with nuclear DNA analysis: one examined penguin fossils from permafrost, in which DNA was unusually well preserved (Shepherd et al. 2005), and the other was a maize study that amplified 50- to 80-bp target genes (Jaenicke-Despres et al. 2003).

The short-tailed albatross *Phoebastria albatrus* is a vulnerable seabird species that is regarded as a management unit, according to IUCN criteria (BirdLife International 2008; U. S. Fish and Wildlife Service 2008). Whereas several millions of birds bred in more than 13 sites in the late 19th century, feather hunting drastically reduced their numbers and caused the extirpation of many breeding sites (Hasegawa 2003; Tickell 2000; U. S. Fish and Wildlife Service 2008). In the mid-twentieth century, only about 50 individuals and one breeding site, Torishima in the Izu Islands (Fig. 1), remained. However, since the cessation of commercial harvesting, the population has grown steadily, and current estimates of world population size are around 3,000 individuals, with about 2,500 birds on Torishima and 500 birds on two islets of the Senkaku Islands (Fig. 1).

In an earlier study, we analyzed mtDNA control region 2 (CR2) of modern short-tailed albatrosses from Torishima and the Senkaku Islands, and found two distinct haplotypic clades, one specific to Torishima and the other distributed across both regions (Eda et al. 2010; Kuro-o et al. 2010). This genetic structure is classified to Phylogeographic pattern II and can be explained by two population history scenarios (Avise 2000): two isolated populations with recent co-occupation on Torishima, or a population with a large evolutionarily effective population size and significant gene flow in which two separate, ancient lineages were retained by chance. Different conservation strategies follow from each scenario; in the first case, the species should be regarded as comprising two different evolutionarily significant units or management units (Moritz 1994), whereas in the second case, the species could be

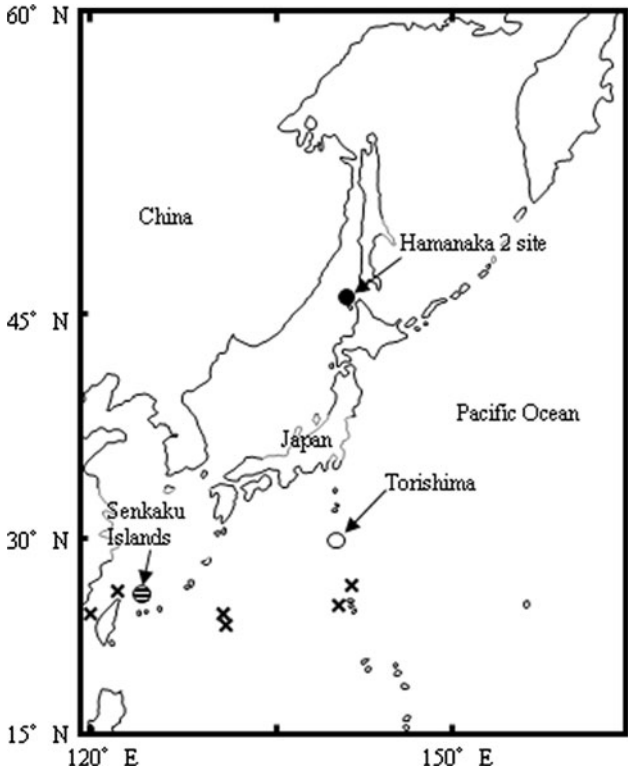

Fig. 1 Distribution of the breeding sites for the short-tailed albatross (Torishima and Senkaku Islands) and sampled archaeological site (Hamanaka 2 site). *X* Former breeding site

managed as a single genetically diverse entity. Therefore knowledge of ancient population structure is important for determining the conservation strategy for this species.

In the previous study, we identified short-tailed albatross bones from Hamanaka 2 site (HM2) on Rebun Island in northern Japan (Fig. 1), using ancient DNA analysis (Eda et al. 2006). Because the bones seemed to result from non-breeding and/or foraging birds harvested by ancient humans at sea (Eda et al. 2005), they were unsuitable for reconstructing ancient population structure via the conventional phylogeographic approach.

In order to investigate the ancient population structure, we obtained mtDNA CR2 sequence, carbon/nitrogen stable isotope ratios and morphological data from each of the archaeological short-tailed albatross samples and combined them in a new approach (see details in materials and methods). In the results, we suggested that short-tailed albatross existed in two populations, between which the genetic distance was greater than that of distinct sister albatross species. Our results suggest that the birds at the present two breeding sites would be descended from these two ancient populations, and that reevaluation of the status and conservation strategy for the species is required.

Materials and methods

Materials

Fifty-eight left-side Diomedeidae carpometacarpi that included the proximal articulate of Os metacarpale majus and minus were collected from HM2 (Eda et al. 2005; Maeda and Yamaura 1992). All of these bones were determined to be about 1,000 years old, because they were found with pottery and stone tools from the Okhotsk period, between the 7 and 12th centuries AD (Maeda and Yamaura 1992). Thirty-five of the 58 samples were also studied in Eda et al. (2006). Using morphological criteria (Eda et al. 2006), 23 of the 58 bones were labeled osteologically mature while the others were considered immature or unknown. In addition, one ulna collected from the Minami-kojima of the Senkaku Islands in May 1996 was analyzed to supplement the scarce sample size for the islands in the previous study (Kuro-o et al. 2010). In total, we analyzed 45 modern samples (41 from Torishima and four from the Senkaku Islands) in the following analysis.

DNA extraction and sequencing

Ancient DNA extractions with precautions to avoid contamination were conducted as described in Eda et al. (2006). The target sequences (CR2 domain I (139 bp) and cytochrome *b* (cyt *b*; 143 bp) from mtDNA) were amplified and sequenced independently for each sample, and authentic sequences were deduced as described in Hofreiter et al. (2001). The extraction was repeated for each sample that shared its CR2 sequence with another sample to be confirmed sample origin. The amplification of cyt *b* was achieved as described in Eda et al. (2006). For the amplification of CR2, semi-nested PCR was done using hot-start Ex*Taq* polymerase (Takara) with the same program used for cyt *b* amplification and the following primers: 1st round, Lcon2.dio (Eda et al. 2010) and Hcon3.dio (5′-TAC CATTCARRGTATGYTGCTCRAGC-3′) and 2nd round, Lcon3.dio (5′-ATTTAATGCATGTACTACGCACATAS AC-3′) or Lcon5.dio (5′-CATTTAATGCATGTACTACG CACATACACATA-3′) and Hcon3.dio. Sequencing was done as described in Eda et al. (2006), using Lcon3.dio, Lcon5.dio and Hcon3.dio. The negative controls yielded no product. Whole DNA was extracted from an ulna collected from the Senkaku Islands as described in Kuro-o et al. (2010), and the CR2 sequences were determined. All sequences have been deposited in DDBJ/EMBL/GenBank under accession numbers AB551841–AB551868.

DNA data analyses

The haplotypes were aligned using ClustalX in MEGA 4.0 (Tamura et al. 2007). A statistical parsimony network for the CR2 haplotypes was generated using TCS version 1.2.1 (Clement et al. 2000) with the sequences from modern short-tailed albatrosses (Kuro-o et al. 2010). Because the nesting algorithm was terminated with the non-parsimonious union of two 4-step clades in the TCS, the least genetic distance between the two clades was calculated using MEGA. The resulting haplotype genealogy was converted to a nested design using a previously described procedure (Templeton and Sing 1993). In this procedure, briefly, haplotypes ("0-step clades") separated by a single substitution were grouped together into "one-step clades" proceeding from the tips to the interior of the haplotype genealogy, then one-step clades by a single substitution were grouped together into "two-step clades", and so on until the next level of nesting would encompass the entire haplotype genealogy. Nucleotide and haplotype diversity was calculated using DnaSP version 5.00.07 (Librado and Rozas 2009). MEGA was employed to calculate inter haplotype group sequence divergence.

Bone measurement and stable isotope analysis

We analysed bone measurements and stable nitrogen/carbon isotope ratios as intrinsic traits that were independent from neutral molecular marker. These traits primarily reflect food availability during the nestling period (e.g. Klicka et al. 1999; Rasmussen 1994), the food chain that the animal belongs to (Deniro and Epstein 1978), and the trophic levels within the food chain (Deniro and Epstein 1981). For bone length, the greatest length of carpometacarpi (Driesch 1976) was measured. For the carbon/nitrogen isotope ratio analyses, collagen was extracted from the samples and measured using ANCA–SL (Europa Scientific Ltd.) as described in Mihara et al. (2002). At least two aliquots (about 0.8 mg of collagen in tin capsules per sample) were combusted in ANCA–SL. The difference between the stable isotope measurements for the various aliquots was 0.08 ± 0.01 for carbon and 0.13 ± 0.01 for nitrogen. Glycine was used as the standard. The purity of the extracted collagen samples was determined by the carbon/nitrogen ratio, calculated from the wt%C by wt%N. The collagen carbon/nitrogen ratios were between 2.94 and 2.95, and fell within the range of "collagen" (DeNiro 1985).

Reconstruction of an ancient population structure

The logic behind the approach is as follows. A random-mating population is defined as all alleles, including neutral and functional ones, distributed randomly among individuals and areas (Futuyma 1986; Hartl and Clark 1997). Intrinsic traits are determined by environmental and/or genetic factors (Futuyma 1986); if traits vary among clades classified by neutral molecular markers, environmental and/or genetic differences should exist between the clades. Differences that arose only through environmental variation imply a geographically structured clade distribution, those that arose through genetic differences imply a structured distribution of functional alleles in particular clades, and those that arose through a combination of environmental and genetic differences imply both a geographically structured clade distribution and structured distribution of functional alleles. In all cases, the assumption of random allele distribution is rejected; therefore, if traits differ among clades, individuals belonging to different clades may form different populations. The null hypothesis (no association between intrinsic markers and the nested group of clades) was examined with respect to the average excess ($a_{i(M)}$; Templeton et al. 1988) and analogous to the clade distance (Templeton 1993).

Let $a_{i(M)}$ be the average excess of the b-step clade, i, nested within $b + 1$ step clade, M. Then,

$$a_{i(M)} = \sum_{K=1}^{n} y_k h_{ik} / \sum_{K=1}^{n} h_{ik} - \sum_{K=1}^{n} y_k h_{Mk} / \sum_{K=1}^{n} h_{Mk}$$

where n refers to the number of individuals, y_k refers to the intrinsic marker value of individual k, and h_{ik} and h_{Mk} refer to the total number of, respectively, clade i and M haplotypes carried by individual k. Let $p_{i(M)}$ be the relative frequency of clade i within clade, M. That is,

$$p_{i(M)} = \sum_{K=1}^{n} h_{ik} / \sum_{K=1}^{n} h_{Mk}$$

Then, the weighted sum of squares of the b-step clades nested within the clade M, $S_{c(M)}$, is

$$S_{c(M)} = \sum_{i} p_{i(M)} a_{i(M)}^2$$

where i is the summed over all b-step clades contained within clade M. In the nested clade analysis, the clade distance is defined as the mean spatial distance of members of a clade from the geographical center of the clade (Templeton 1993). Similar to the distance, we calculated $V_{(i)}$, the variance of intrinsic markers for all individuals of each b step clade, i.

The significance was calculated by comparison with a null distribution constructed from 5,000 random permutations against the intrinsic marker values as described by Templeton et al. (1995) and Templeton & Sing (1993) using R 2.10.1 (R Development Core Team 2009). Null distributions were constructed by randomizing the data table for each $b + 1$ step clade, M, in which haplotype frequencies and sample

sizes were preserved, and estimating again the test statistics (i.e. $S_{c(M)}$ and $V_{(i)}$) for each randomized data set. These tests are asymptotically independent, both at the same clade level and across clade levels because of the nested design (Prum et al. 1990; Templeton and Sing 1993).

Results

The target sequence in CR2 was successfully isolated in 46 of 58 (79.3%) bones collected from HM2, and 32 polymorphic sites defining 28 haplotypes were found. A statistical parsimony network clearly showed two haplotypic groups (Fig. 2): group 1, which included 19 haplotypes from 38 chicks on Torishima and nine haplotypes from 15 archaeological bones, and group 2, which included two haplotypes from three chicks on Torishima, one haplotype from four samples on the Senkaku Islands and 18 haplotypes from 31 archaeological bones. Using a nested-clade approach, the entire haplotype genealogy was included in two 4-step clades. The target sequence in cyt *b* was successfully isolated in 42 bones (73.7%) in which all samples determining CR2 sequence were included. One polymorphic site defining two haplotypes was found, as previously described in Eda et al. (2006). Each of the 4-step clades in CR2 corresponded to the cyt *b* haplotypes without any inconsistency (Supplementary material).

For the entire data set, a null hypothesis of no association between intrinsic markers and clades between clades 4–1 and 4–2 was rejected. The carpometacarpi length and nitrogen isotope ratio (δ^{15}N) were significantly different between the clades (for bone length and δ^{15}N, $P < 0.05$). Within clade 4–2, the clade distances, or variances in bone length and δ^{15}N, were significantly smaller than for the randomly extracted samples ($P < 0.01$). The null hypothesis was not rejected at any other clade level. The results remained unchanged if immature and age-unknown sample data were excluded, except for clade distance of bone length within clade 4–2 (not significant).

For the ancient samples, the haplotype and nucleotide diversities were, respectively, 0.857 (±0.09, SD) and 0.02556 (±0.00462) for the clade 4–1 population and 0.933 (±0.03) and 0.03964 (±0.00304) for the clade 4–2 population (Fig. 3). For the modern samples, the haplotype and nucleotide diversities were, respectively, 0.925 (±0.025) and 0.03180 (±0.00202) for the haplotypes belonging to clades 4–1 and 0.667 (±0.160) and 0.03357 (±0.00895) for the haplotypes belonging to clades 4–2. Similar levels of nucleotide diversity were found for the ancient and modern sample, suggesting a lack of post-mortem genetic degradation causing artifactual mutations. Sequence divergence between the two haplotypic groups was 11.5%.

Discussion

Ancient population structure

CR2 and cyt *b* sequences clearly show two haplotypic clades, between which a null hypothesis of no association between intrinsic markers (nitrogen isotope ratio and bone length) and clades was rejected. These facts suggest that individuals having mtDNA belonging to the same haplotypic clade formed a different population about 1,000 years ago, and they strongly support a historical scenario explaining the modern genetic structure: the co-occupation of populations isolated for long periods of time. Judging from the current haplotype frequencies at the breeding regions, Torishima and the Senkaku Islands would have been mostly occupied by, respectively, clade 4–1 and 4–2 lineage birds. Unfortunately, there is no data that prove a relict population of albatrosses survived at the Senkaku Islands: from 1910 to the 1970s (a period almost equivalent to the maximum longevity), no chicks were observed on the Senkaku Islands, and furthermore, no individuals had been observed on or near the Islands from 1939 to 1971, despite several biological surveys during the breeding season (1939, 1950, 1952, 1963, 1970, 1971, 1979 and 1980) (Hasegawa 2003). However, the number of birds surviving on the Senkaku Islands is presumed to have been very small, even compared with Torishima where the population was reduced to around 50 birds (Hasegawa 2003; Tickell 2000; U. S. Fish and Wildlife Service 2008). Given the breeding location of the species (mid-point or tops of cliffs) and the short survey periods for each island, it is possible that this very small population was overlooked.

Genetic difference between two populations

Although no subspecies of *P. albatrus* have been proposed, the sequence divergence between the two clades (11.5%) is greater than that between recognized sister species of albatrosses analyzed for CR domain I: 1.0% for *Diomedea antipodensis* and *D. gibsoni*, 1.8% for *Thalassarche cauta* and *T. steadi*, 2.9% for *T. salvini* and *T. eremita*, 4.5% for *D. exulans* and *D. dabbenena*, 4.6% for *D. exulans* and *D. amsterdamensis*, and 7.2% for *T. melanophris* and *T. impavida* (Abbott and Double 2003; Burg and Croxall 2001, 2004; Rains et al. 2011). Since the degree of divergence between the two *P. albatrus* populations is larger than that between *T. melanophris* and *T. impavida*, the relationship between the two populations on Torishima is analogous to that observed between *T. melanophris* and *T. impavida* on Campbell Island, which includes incomplete assortative mating and outbreeding depression (Moore et al. 1997). Sympatric breeding revealed by mtDNA analysis does not

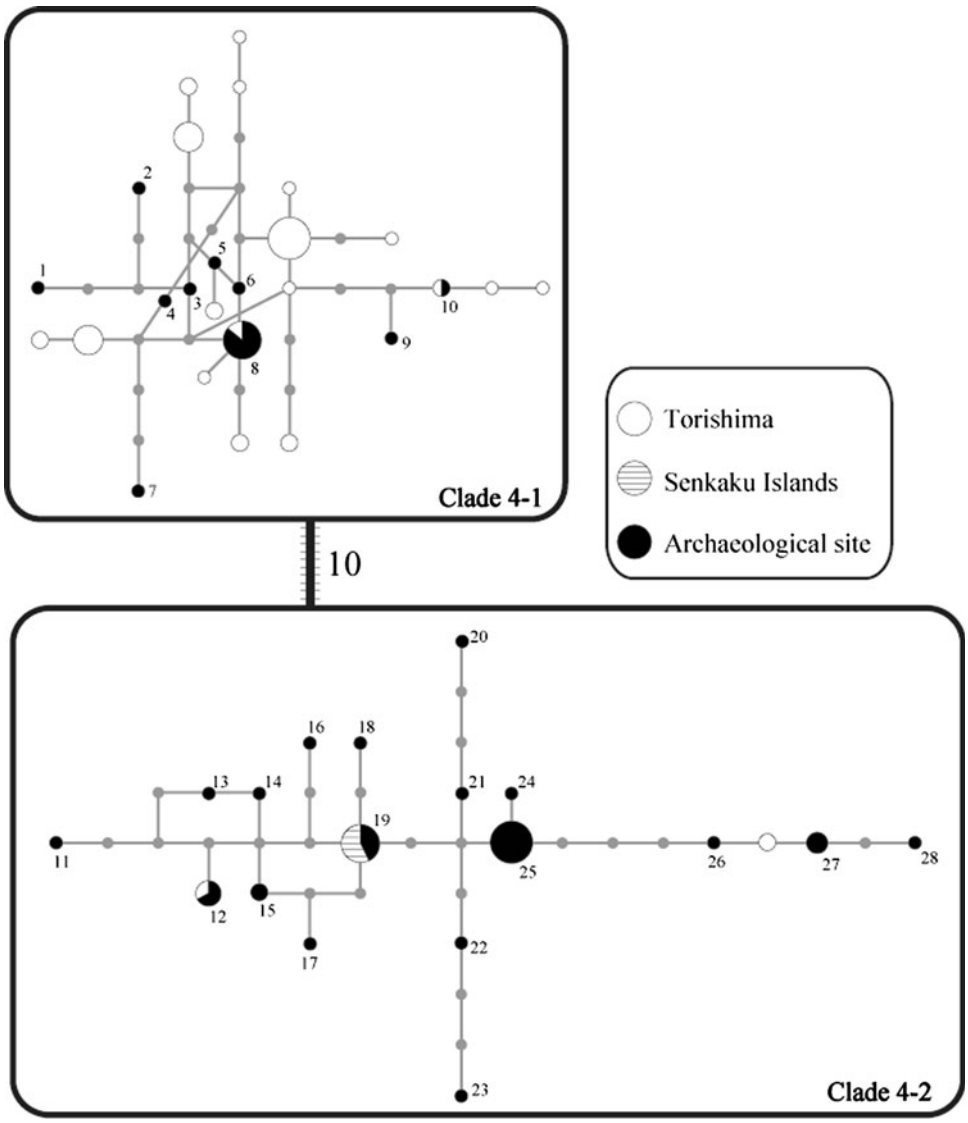

Fig. 2 The statistical parsimony network of the haplotype from archaeological (Hamanaka 2 site; $N = 46$) and living short-tailed albatrosses (Torishima, $N = 41$; Senkaku Islands, $N = 4$). The size of each circle is proportional to the number of albatrosses sharing that haplotype. Numbers in the network show haplotype name corresponding to supporting information

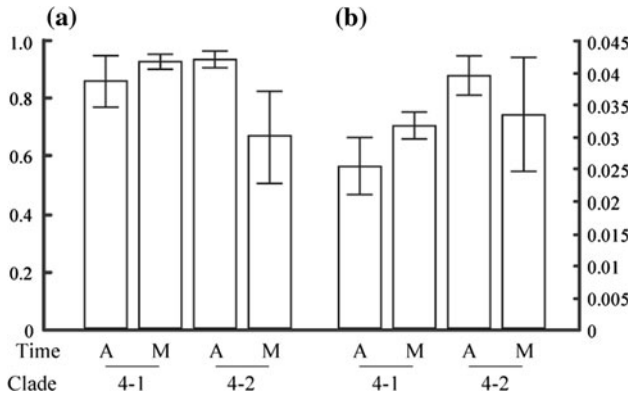

Fig. 3 Haplotype (**a**) and nucleotide diversity (**b**) for ancient (*A*) and modern (*M*) samples from clade 4–1 and 4–2 birds. *Error bars* show standard deviations

imply mating between individuals from the two populations. Pre-mating isolation is suggested by differences in courtship display between ringed (known to have fledged from Torishima) and un-ringed young birds (likely fledged from the Senkaku Islands) and the difference in breeding season (about 2 weeks earlier on the Senkaku Islands; H. Hasegawa, personal observation). On Torishima, one or two developmentally disabled chicks were observed each year beginning in the late 1990s (Hasegawa 2003), but they became rare in the late 2000s (H. Hasegawa, personal observation). Because the chicks were observed at a similar position in the colony (Hasegawa 2003), their disability may have been genetic in origin. Outbreeding depression rather than inbreeding depression would be a reasonable mechanism since currently the haplotype diversity on Torishima is high (Kuro-o et al. 2010) and the genetic distance between the lineages is greater than that between *T. melanophris* and *T. impavida*,

for which outbreeding depression has been suggested (Burg and Croxall 2001; Moore et al. 1997).

Difference in genetic diversities among modern and ancient populations

The ranges of haplotype diversity for the two ancient populations overlapped and were not significantly different. However, the ranges in nucleotide diversity did not overlap, indicating a significant difference between the two populations. These observations suggest that the populations had maintained stable numbers of individuals for a long time and that the origin of the clade 4–2 population predates the clade 4–1 population.

For the haplotypes belonging to clade 4–1, the haplotype diversity overlapped between the ancient and modern samples and was not significantly different. This similarity in haplotype diversity is consistent with population genetic simulations predicting a minor reduction in haplotype diversity among the birds on Torishima, given the short amount of time (relative to generation time) during which the population numbers were severely depressed (Kuro-o et al. 2010). In contrast, the haplotype diversities did not overlap between the ancient and modern samples for those haplotypes belonging to clade 4–2, suggesting a significant loss of genetic diversity in this lineage. This observation is concordant with the model in which a small number of birds survived the commercial harvest era on the Senkaku Islands. One would expect the loss of genetic diversity to have been greater than that shown in Fig. 3 since birds in that lineage do not seem to mate randomly; they breed on Torishima and the Senkaku Islands, and no evidence of emigration from Torishima to the Senkaku Islands has been observed (nearly all Torishima birds are fitted with metal leg bands as chicks since 1979, and no banded birds observed on the Senkaku Islands in 1980, 1988, 1991, 1992, 1996, 2001 and 2002; H. Hasegawa, personal observation).

Lessons for conservation strategies of the short-tailed albatross

Given our results, we conclude that two populations of the short-tailed albatross existed about 1,000 years ago, and that the level of genetic divergence exceeded that between sister species of other albatrosses. The exact point at which the two lineages began to co-distribute on Torishima is unknown; however, after the early 20th century (i.e. after massive population decline of the species) is a reasonable assumption. In the wandering albatross, the proportion of juveniles recruited to the natal population is suggested to be positively related to population size (Inchausti and Weimerskirch 2002). If this trend is true for the short-tailed albatross, the dispersal rate from the Senkaku Islands and emigration rate to Torishima is expected to have increased during the early 20th century when few birds survived on the Senkaku Islands. Although during the late 19th and early 20th centuries the species was exterminated at most breeding colonies, descendents of each population survived at both locations. The species is considered to be vulnerable and a management unit. Biparental molecular marker analyses (e.g. microsatellite DNA) of the birds on Torishima are required to assess whether the two populations are mixing. In 2008, to create a third stable breeding station, the translocation of chicks from Torishima 350 km south to Mukojima of the Bonin Islands was begun as an international conservation project (U. S. Fish and Wildlife Service 2008). To exclude the risk of artificial population admixture and outbreeding depression, genetic monitoring of the chicks on Torishima using mtDNA or microsatellite DNA and careful selection of the individuals to be translocated are required. Furthermore, genetic diversity among the clade 4–2 lineage birds was drastically decreased through exploitation during the late 19th and early 20th centuries. Careful and extensive study of the Senkaku Islands birds, which has not been conducted since the 2001–2002 breeding season due to territorial disputes among the neighboring countries, is therefore necessary.

Future perspectives of the ancient population structure and conservation biology

The approach used in our study proved useful for reconstructing the ancient population structure of the short-tailed albatross. This approach may be useful for inferring the ancient population structures of highly mobile animals captured within or outside their breeding area, and in classifying recently mixed or sympatrically diverged populations. It is possible to apply this approach to other species for which there is no information on breeding-site location. For example, we can infer population structure from archaeological remains or the fossils of animals that were traded, such as large herbivores, and of animals that are highly mobile, like migratory birds, whales, and fishes. The reconstructed ancient population structure would be useful for conservation and management recommendations. In addition, when more than one population is detected, the temporal change of the genetic diversity can be compared among populations. The information will be useful to assign conservation priority to each population. In this study, we analysed bone measurements and stable nitrogen/carbon isotope ratios as intrinsic traits that were independent from neutral molecular marker. In addition to these traits, stable isotopes of hydrogen (δD; Hobson and Wassenaar 1997; Chamberlain et al. 1997; Lott et al. 2003; Clegg et al. 2003), strontium (δ87Sr; Chamberlain et al. 1997), and sulphur (δ34S; Lott et al. 2003) have been used

to reveal the connectivity of breeding and non-breeding areas in migratory animals (reviewed in Hobson 1999; Webster et al. 2002). In particular, analyses of stable isotope ratios of hydrogen, which display an approximate latitudinal gradient (Hobson and Wassenaar 1997), and those of strontium, which correspond with those found in regional soil parent materials (Chamberlain et al. 1997), may improve the power to reconstruct ancient population structures in other animals. The most important lesson from zooarchaeological short-tailed albatross bones would be that the ancient population structure can be reconstructed from zooarchaeological remains and that the reconstructed population structure is useful for conservation and management recommendations.

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