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Predominance of unbalanced gene flow from the western to central North Pacific colonies of the Black-footed albatross (*Phoebastria nigripes*)

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Abstract

The Black-footed albatross (*Phoebastria nigripes*) breeds in two remote regions, approximately 4,000 km apart, in the North Pacific. The population in the central North Pacific region (Northwestern Hawaiian Islands), which contains >95% of the total population, is currently stable, although concerns exist over future declines. In contrast, the population in the western North Pacific (Izu and Ogasawara Islands in Japan) is rapidly increasing, and the breeding areas are expanding. To estimate possible gene flow caused by dispersal between populations, we performed genetic analysis on six colonies of Black-footed albatross using 10 microsatellite markers. The central and western North Pacific populations were genetically differentiated. However, an estimation of migrants per generation indicated directional dispersal from the western to the central North Pacific. In particular, the population on Kure Atoll, the westernmost atoll in the Hawaiian Islands in the central North Pacific, exhibited weak genetic differentiation from the western North Pacific populations, suggesting frequent immigration from the western North Pacific. The recent expansion of the western North Pacific population may be due to an increase in returning individuals, which may be caused by increased breeding success rates and/or survival rates. Range-wide and long term monitoring of the Black-footed albatross population using genetic markers may help to uncover the dispersal dynamics of this highly mobile but philopatric albatross species and to make appropriate conservation decisions in light of environmental changes.

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Introduction

For a highly mobile albatross species, the open ocean is not necessarily a geographical barrier that restricts dispersal (Weimerskirch and Wilson 2000, Croxall et al. 2005, Phillips et al. 2005). Long-range dispersal events may also influence the population dynamics of remote breeding colonies (Young 2010), which could be reflected by their population genetic structure, as estimated by highly variable markers (Rousset 2001). Several previous studies have reported gene flow among remote breeding colonies of albatross species (Burg and Croxall 2001, 2004, Abbott and Double 2003, Bekkum et al. 2006, Huyvaert and Parker 2006, Milot et al. 2008, Young 2010, Ando et al. 2011), despite their strong nest fidelity and natal philopatry (Tickell 2000). Information on the genetic structure of populations is important for determining dispersal dynamics and thus conservation planning for highly pelagic species.

The major breeding colonies of the Black-footed albatross, *Phoebastria nigripes*, are restricted to two remote regions, approximately 4,000 km apart, in the North Pacific (BirdLife International 2012). The colony in the Northwestern Hawaiian Islands in the central North Pacific is currently stable and holds more than 95% of the total population (approximately 59,000 pairs), distributed among eight breeding colonies. Future declines due to fishery bycatch and colony loss by sea level rise are a concern (Arata et al. 2009). In contrast, the populations in the western North Pacific, in the Izu Islands (approximately 1,000 pairs) and the Ogasawara Islands (approximately 1,000 pairs), are rapidly increasing and expanding (Arata et al. 2009, Tokyo prefecture 2008, Suzuki et al. unpublished data), while the trend of another colony in the Senkaku Islands (56 pairs, Arata et al. 2009) is unknown. Indeed, the number of breeding pairs in the Ogasawara Islands has tripled in the last decade (Suzuki et al. unpublished data).

Previous genetic studies using mitochondrial cytochrome *b* sequences indicated genetic differentiation between the central and western North Pacific populations (Walsh and Edwards

2005, Eda et al. 2008). Thus, the recent expansion of the western North Pacific population may be due to increasing natal recruitment of individuals from the western North Pacific population itself, rather than to immigration from the central North Pacific population. However, the degree of gene flow between the two regions is still unresolved. Several sampled individuals in the western North Pacific colonies exhibited haplotypes common to the central North Pacific population (Walsh and Edwards 2005, Eda et al. 2008), and thus, Eda et al. (2008) suggested that gene flow between the two regions should not be ignored. The results of a microsatellite analysis performed among breeding colonies in the Ogasawara Islands also indicated immigration from outside of the Ogasawara Islands (Ando et al. 2011). All of the above studies targeted a limited number of breeding colonies and had small sample sizes; thus, these studies may have provided only fragmented information about the genetic structure of the Black-footed albatross. In the case of the sympatrically distributed Laysan albatross, *P. immutabilis*, no clear genetic differentiation between the central and western North Pacific region was found, indicating that long-range dispersal may occur between the two regions in the North Pacific (Young 2010). Thus, similar results could be expected in the range-wide genetic analysis of the Black-footed albatross using highly variable nuclear markers.

The present study sought to estimate recent possible gene flow between the central and western North Pacific populations of the Black-footed albatross. We targeted all of the major breeding colonies of the species and performed a genetic analysis using polymorphic microsatellite markers.

Materials and methods

Sampling and DNA extraction

Feather or blood samples were collected from 278 Black-footed albatross chicks or breeding adults at six breeding colonies on the following islands: Izu-Torishima (50) and the Ogasawara Islands (77) in the western North Pacific and Kure Atoll (11), Midway Atoll (48), Laysan Island (44) and Tern Island (48) in the central North Pacific from 2003 to 2008 (Fig. 1). Samples in the Ogasawara Islands were analyzed in Ando et al. (2011). The collected samples were stored at -30 °C before DNA extraction. DNA of the Izu-Torishima samples was extracted according to the SDS/Proteinase K protocol (Sambrook and Russell 2001). For the samples from the central North Pacific, DNA was extracted from tissue and feathers using Qiagen DNeasy ™ extraction kits (Qiagen, Valencia, CA, USA) following the manufacturer's protocols, and DNA from blood was isolated using ID Labs IDetect ™ DNA purification kits for whole animal blood (ID Labs Biotechnology Inc., London, ON, Canada) following the manufacturer's protocols.

<Fig. 1 about here>

Microsatellite analysis

The genotypes of the sampled individuals were determined at ten polymorphic microsatellite loci (Dc5, Dc9, Dc20 and De11: Burg 1999, 10C5, 11F3, 11H1, 11H7, 12C8 and 12H8: Dubois et al. 2005) isolated from the Wandering albatross, *Diomedea exulans*. PCR amplification was carried out using a Qiagen Multiplex PCR kit (Qiagen K.K. Tokyo, Japan). Each 10 mL total volume of the reaction mixture contained 5 ng of extracted DNA, 5 mL of 2x Multiplex PCR Master Mix and 0.2 mM of each primer pair. The PCR conditions were as follows: first denaturation for 15 min at 95 °C, 25 cycles of 30 s at 94 °C, 1.5 min at 57 °C and 1 min at 72 °C and a final cycle for 30 min at 60 °C. The sizes of the PCR products were measured using the ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA), GeneScan and Genotyper analysis software (Applied Biosystems).

Data analysis

The number of alleles per locus (N_A), allelic richness (R_S), and expected (H_E) and observed heterozygosities (H_O) were calculated to quantify genetic diversity. The number of alleles per locus and the expected and observed heterozygosities were calculated using GENALEX 6 (Peakall and Smouse 2006), and allelic richness was calculated using FSTAT 2.9.3 (Goudet 2001). The difference in allelic richness between the central and western North Pacific groups, departures from Hardy–Weinberg Equilibrium (HWE) and linkage disequilibrium were tested using FSTAT. We also listed private alleles in each region and in the population. To estimate the hierarchical genetic structure of each population, an analysis of molecular variance (AMOVA, Excoffier et al. 1992) based on F_{ST} and R_{ST} was performed using GENALEX 6. Genetic variances were partitioned at three levels: between the western and central North Pacific populations, among populations within regions, and within populations. The F_{ST} and R_{ST} values between each pair of populations were calculated, and their deviation from zero was tested using FSTAT. We performed individual-based clustering STRUCTURE analysis using the STRUCTURE 2.2.3 software (Prichard et al. 2000). In this method, the appropriate number of genetic groups (clusters: K) is estimated based on log likelihood, and individuals are assigned to the most likely cluster. We used admixture with LOCPRIOR and allele frequency correlated models. Ten runs of K = 1–8 were carried out with 1,000,000 Markov Chain Monte Carlo (MCMC) and 100,000 burn-in repetitions. Based on the correlated allele frequency model, the amount of divergence for each cluster from a common ancestral population was calculated (F values, Falush et al. 2003). The number of migrants per generation among populations was estimated using a maximum-likelihood approach in the software Migrate 3.1.5 (Beerli and Felsenstein 1999, 2001). We used a Brownian motion mutation model with constant mutation

rates over loci, and each MCMC run consisted of 10 short and three long replicate chains. The burn-in period was set to 100,000 steps.

<Table 1 and Table 2 about here>

Results

The genotypes of 278 individuals were determined at ten microsatellite loci. The estimators of genetic diversity in each population (N_A, R_S, H_E and H_O) are shown in Table 1. Each population exhibited a similar level of genetic diversity, despite large differences in population sizes. Some populations have private alleles (Fig. 1, Table 1, Table 2). The allelic richness was not significantly different between the central and western North Pacific groups (P = 0.134). There were no departures from HWE at each microsatellite locus, and there was no evidence of linkage disequilibrium among any pairwise microsatellite loci comparisons. In the AMOVA, six percent of the genetic variance was attributed to variance between regions, and both the F_{ST} and R_{ST} values were significantly different from zero (Table 3). Comparing pairwise F_{ST} values among populations, the central and western North Pacific populations were clearly genetically differentiated (Table 4). In contrast, the R_{ST} values between Kure in the central North Pacific and Ogasawara and Izu in the western North Pacific were not significantly larger than zero (Table 4). In fact, the R_{ST} values between Kure and all other populations were not significantly different from zero. In the STRUCTURE analysis, the log likelihood was maximized at K = 2 (Fig. 2). From K = 3 to K = 8, the standard deviations increased. When K = 2, the central and western North Pacific populations were clearly assigned to different clusters (Fig. 3). However, the cluster that dominated in the western North Pacific population appeared in

larger proportion in the Kure population than in the other populations in the central North Pacific. The *F* values of each cluster were nearly the same. The number of migrants per generation estimated using Migrate 3.1.5 is shown in Table 5. Significantly larger numbers of migrants were estimated from Ogasawara and Izu in the western North Pacific to each population in the central North Pacific compared to the opposite direction.

<Table 3, Table 4, Table 5, Fig. 2 and Fig. 3 about here>

Discussion

Genetic characteristics and population history of the western North Pacific population

The results of the AMOVA, the F_{ST} values and the STRUCTURE analysis suggested that the central and western North Pacific populations are clearly genetically differentiated. These results are consistent with previous studies comparing mitochondrial cytochrome *b* sequences between the populations (Walsh and Edwards 2005, Eda et al. 2008). In addition, both the western and central North Pacific populations had several private alleles and exhibited similar levels of genetic diversity. Black-footed albatross in the western North Pacific seem to have maintained a genetically unique population, despite the serious population decline due to human disturbance in the late 19th and early 20th centuries (e.g., overexploitation for feathers and meat, Yamashina 1930, 1942, Cousins and Cooper 2000, Tickell 2000). This may be because many of the individuals, particularly non-breeders, survived the overexploitation on the sea and maintained their genetic diversity. Rapid population recovery after the population bottleneck could prevent further loss of genetic diversity due to genetic drift. The above situation could be possible for the long lived (40 or more years) late maturing (starts breeding at 7 years old) Black-footed albatross (Cousins and Cooper 2000). A similar situation was reported in the Short-tailed albatross, *P. albatrus*, whose breeding population had been reduced to 50 – 60 individuals in the

1940s in the Izu Islands (Hasegawa 2003, Tickell 2000) but has maintained high genetic diversity (29 haplotypes in mitochondrial control region, Kuro-o et al. 2010).

The results of the present study suggest that recent population growth and expansion of the western North Pacific population is not due to immigration from the central North Pacific population but due to natal recruitment from the western North Pacific breeding colonies, as previous studies indicated (Walsh and Edwards 2005, Eda et al. 2008). This suggestion is supported by the estimated number of immigrants from the central North Pacific (0.0002 – 1.6727, Table 5), which is much smaller than the actual increase of the breeding population in the last two decades (Suzuki et al. unpublished data). The increased natal recruitment in the western North Pacific population is likely a combination of high reproductive success rates (fledging success: 93%, Deguchi et al. 2011) and/or high post-fledging survival. In the Ogasawara Islands, nesting conditions seem to have improved after the eradication of feral goats, carried out in 2004 (Hasegawa 1992, Tokyo Prefecture 2008). This eradication may have increased the breeding success rate of the Black-footed albatross in the Ogasawara Islands. However, the population of the Laysan albatross, which use the same nesting site as the Black-footed albatross in the Ogasawa Islands, has not increased from 10-20 pairs (Oka 1995, Tokyo Prefecture 2008) after first recognition of breeding in 1976 (Kurata 1978). The reason for this discrepancy is unclear. To understand the basis of the population increase and expansion of the Black-footed albatross in the western North Pacific, an analysis of reproductive success, survival, and foraging areas in the breeding and non-breeding season is required, including comparisons with the populations of the central North Pacific and other North Pacific albatross species.

Inferred long dispersal between the central and western North Pacific populations

The results of our Migrate analysis indicated a large number of migrants exist from the western North Pacific to the central North Pacific. Our calculated values were much higher than those of previous studies using mitochondrial cyt*b* sequences (Walsh and Edwards 2005, Eda et al. 2008). This result may indicate the long dispersal of the western North Pacific population. The genetic structure of the Kure population in the central North Pacific may reflect immigration from the western North Pacific population, indicated by the larger number of estimated immigrants per generation from both Ogasawara and Izu in the western North Pacific. Our R_{ST} values and STRUCTURE analysis also indicated weak genetic differentiation between the Kure and western North Pacific populations. In STRUCTURE analysis, all of the sampled individuals on Kure were assigned to the western North Pacific cluster with a higher probability (0.075 – 0.548) than the other individuals sampled in the central North Pacific, except for one individual from Midway (0.109). In contrast, none of the sampled individuals in the western North Pacific population, including the two genetically distinct individuals observed by Ando et al. (2011), were assigned to the central North Pacific cluster with a high probability (< 0.033). The two genetically distinct individuals do not appear to be related to immigrants from the central North Pacific population but seem to belong to a minor strain in the Ogasawara Islands or to immigrants from Senkaku Islands, where genetic study has never been conducted. Long dispersal may occur easily in the western North Pacific population, similar to a previous study of the Wandering albatross (Gauthier et al. 2010). Gauthier et al. (2010) found that the smallest colony had the highest number of dispersing young because of the low availability of potential mates. Although the population size of the Black-footed albatross in the western North Pacific colonies is increasing, the colony is still small and of low density compared with the major breeding colonies in the central North Pacific (Arata et al. 2009, Tokyo Prefecture 2008). Thus, dispersal of young individuals may be occurring, even over the long distances (approximately 4,000 km)

between the western and central North Pacific colonies. This may be possible because the population distribution during the non-breeding season on each side of the North Pacific overlaps (Cousins and Cooper 2000, Tickell 2000). Gauthier et al. (2010) also suggested that most dispersers colonize in a colony where the density is the lowest. Young dispersers from the western North Pacific colonies might easily colonize the Kure Atoll, which exhibits a small population size and low density (Arata et al. 2009).

Migration between the central and western North Pacific populations has been discussed in two previous studies that assessed mitochondrial DNA sequences (Walsh and Edwards 2005, Eda et al. 2008). Eda et al. (2008) suggested the existence of low but apparent migration between the regions. However, the present study, using highly variable microsatellite markers and wide sampling, including the Kure Atoll, indicated more frequent and directional dispersal between each side of the North Pacific.

Implications for conservation and future studies

The present study revealed that the recent increase and expansion of the western North Pacific population of the Black-footed albatross was not due to immigration from the central North Pacific population. The western North Pacific population, which exhibits unique genetic characteristics and a small population size, should be regarded as a high conservation priority. The present study also suggested the existence of gene flow between each side of the North Pacific at an island population level, indicating a recent long dispersal. Thus, whether each population is to be regarded as a separate species, as Walsh and Edwards (2005) suggested should be decided after careful comparison of morphology or other ecological differences. However, the genetic structure of the Black-footed albatross may change in the future, depending on population trends. In 2011, the low lying colonies in the central North Pacific were strongly

damaged by the 11 March tsunami as well as by prior storm surges that season. At least 110,000 of the Laysan and Black-footed albatross chicks and at least 2,000 adults were killed on Midway Atoll (USFWS 2011). In contrast, the high lying western North Pacific colonies were not damaged and continued to expand. This may promote gene flow from the western North Pacific to the central North Pacific. However, if further loss of low lying colonies in the central North Pacific occurs due to sea level rise, as Baker et al. (2006) noted, the western North Pacific colonies may function as refugia for the central North Pacific population. In this case, gene flow from the central to the western North Pacific may accelerate. Range-wide and long-term monitoring of Black-footed albatross populations using both empirical observations and genetic data may help to characterize the complex dispersal dynamics of this highly mobile but philopatric albatross species and to craft an appropriate conservation strategy that incorporates environmental changes.

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Table 1 Genetic diversity of the six populations of Black-footed albatross based on microsatellite data: the number of individuals (n), number of alleles per locus (N_A), allelic richness (R_S), and expected (H_E) and observed (H_O) heterozygosities for 10 microsatellite loci in the six populations.

	Microsatellite loci										
	10C5	11F3	11H1	11H7	12C8	12H8	Dc5	Dc9	Dc20	De11	Ave.
Tern (n = 48)											
N_A	3	1	9	11	4	1	4	3	2	7	4.5
R_S	2.69	1.00	6.64	8.27	2.64	1.00	3.21	2.61	1.65	5.54	3.52
H_E	0.26	0.00	0.77	0.84	0.52	0.00	0.50	0.27	0.08	0.62	0.39
H_O	0.27	0.00	0.73	0.92	0.54	0.00	0.42	0.31	0.08	0.56	0.38
Laysan (n = 44)											
N_A	3	1	9	9	2	1	3	4	2	7	4
R_S	1.83	1.00	6.81	7.15	2.00	1.00	2.69	3.31	1.83	4.48	3.21
H_E	0.09	0.00	0.78	0.80	0.49	0.00	0.44	0.45	0.13	0.55	0.37
H_O	0.09	0.00	0.75	0.73	0.57	0.00	0.39	0.41	0.14	0.64	0.37
Midway (n = 48)											
N_A	3	1	9	10	4	1	3	4	2	8	5
R_S	2.45	1.00	6.95	7.05	3.56	1.00	2.86	2.98	1.75	5.47	3.51
H_E	0.21	0.00	0.81	0.80	0.61	0.00	0.50	0.41	0.10	0.67	0.41
H_O	0.23	0.00	0.79	0.77	0.47	0.00	0.51	0.38	0.11	0.66	0.39
Kure (n = 11)											
N_A	3	1	8	5	2	1	3	3	1	4	3.1
R_S	3.00	1.00	8.00	5.00	2.00	1.00	3.00	3.00	1.00	4.00	3.10
H_E	0.24	0.00	0.84	0.65	0.46	0.00	0.42	0.17	0.00	0.63	0.34
H_O	0.27	0.00	1.00	0.64	0.36	0.00	0.45	0.18	0.00	0.55	0.35
Bonin (n = 77)											
N_A	3	2	9	10	2	2	5	3	2	5	4.5
R_S	2.14	1.14	6.78	7.28	1.99	1.37	3.19	2.92	1.27	3.42	3.15
H_E	0.33	0.01	0.79	0.83	0.28	0.04	0.30	0.41	0.03	0.59	0.36
H_O	0.34	0.01	0.81	0.84	0.05	0.04	0.30	0.38	0.03	0.51	0.32
Izu (n = 50)											
N_A	4	1	8	8	2	1	4	3	3	4	3.8
R_S	2.44	1	6.55	5.91	1.99	1	2.91	2.98	1.92	2.61	2.93
H_E	0.40	0.00	0.77	0.78	0.30	0.00	0.35	0.50	0.10	0.52	0.37
H_O	0.48	0.00	0.86	0.82	0.20	0.00	0.38	0.48	0.06	0.52	0.38
All (n = 278)											

N_A	4	2	10	13	5	2	6	4	3	9	5.8
R_S	2.55	1.04	6.87	7.50	2.53	1.12	3.03	2.98	1.64	4.50	3.38
H_E	0.26	0	0.79	0.78	0.44	0.01	0.42	0.37	0.07	0.6	0.38
H_O	0.28	0	0.82	0.79	0.37	0.01	0.41	0.36	0.07	0.57	0.37

[Table 1 cont'd]

Table 2 Private alleles in each region and population

Region	Population	Locus	Allele size (bp)	Frequency
West	Midway	11H7	215	0.01
West	Midway	12C8	223	0.04
West	Tern	12C8	261	0.01
West	Tern	Dc05	176	0.02
Central	Ogasawara	11F3	240	0.01
Central	Ogasawara	11H7	194	0.01
Central	Ogasawara	12H8	167	0.02
Central	Ogasawara	Dc05	173	0.01
Central	Ogasawara	De11	200	0.01
Central	Izu	10C5	171	0.01
Central	Izu	Dc20	112	0.02

Table 3 AMOVA results based on F_{ST} and R_{ST}

	d.f.[1]	SS[2]	Var.[3]	%[4]	
F_{ST}					
Between regions	1	35.287	0.119	6%	F_{ST}=0.062 (P=0.001)
Among populations within regions	4	9.613	0.006	0%	N_{em} = 3.78
Within populations	548	1041.511	1.901	94%	
R_{ST}					
Between regions	1	1382.46	4.84	6%	R_{ST} = 0.052 (P=0.001)
Among populations within regions	4	240.76	0.00	0%	
Within populations	548	45442.16	82.92	94%	

[1]d.f.: degree of freedom, [2]SS: sum of squares, [3]Var: genetic variability, [4]%: percentage variability

Table 4 Pairwise F_{ST} (above diagonal) and R_{ST} (below diagonal) values

	Tern	Laysan	Midway	Kure	Ogasawara	Izu
Tern	_	0.004	0.000	0.012	0.073*	0.073*
Laysan	0.000	_	0.004	0.014	0.065*	0.066*
Midway	0.000	0.002	_	0.000	0.054*	0.055*
Kure	0.000	0.000	0.000	_	0.030*	0.043*
Ogasawara	0.059*	0.064*	0.042*	0.000	_	0.002
Izu	0.062*	0.065*	0.040*	0.003	0.000	_

* $P < 0.01$

Table 5 The number of migrants per generation between each pair of populations as estimated with the maximum likelihood estimation (MLE) with 95% CI.

		2.5%	MLE	97.5%
From	To			
Midway	Laysan	0.002	0.003	0.004
	Tern	0.034	0.037	0.042
	Kure	0.025	0.028	0.032
	Ogasawara	0.010	0.012	0.015
	Izu	0.011	0.013	0.015
Laysan	Midway	0.000	0.000	0.000
	Tern	0.000	0.000	0.000
	Kure	0.000	0.000	0.000
	Ogasawara	0.000	0.000	0.000
	Izu	0.000	0.000	0.000
Tern	Midway	0.027	0.032	0.037
	Laysan	0.012	0.015	0.019
	Kure	0.034	0.040	0.045
	Ogasawara	0.046	0.052	0.059
	Izu	0.016	0.020	0.024
Kure	Midway	0.902	1.008	1.122
	Laysan	0.655	0.746	0.846
	Tern	0.120	0.161	0.209
	Ogasawara	0.008	0.019	0.038
	Izu	1.534	1.673	1.819
Ogasawara	Midway	0.296	0.399	0.525
	Laysan	1.489	1.715	1.963
	Tern	0.481	0.611	0.764
	Kure	4.101	4.474	4.868
	Izu	1.151	1.350	1.571
Izu	Midway	4.257	4.717	5.209
	Laysan	3.880	4.318	4.789
	Tern	0.423	0.572	0.754
	Kure	3.703	4.131	4.592
	Ogasawara	4.021	4.468	4.946

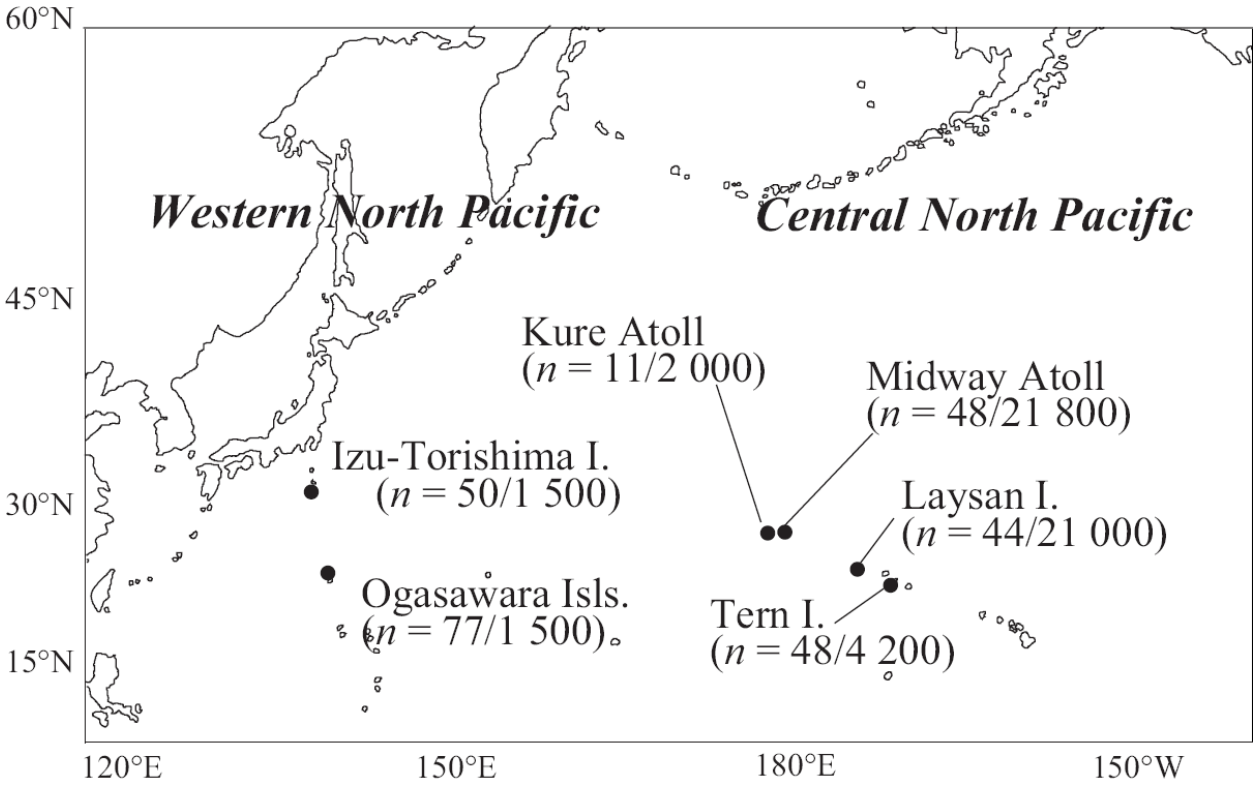


Fig. 1 Sampling locations in the central and western North Pacific colonies of the Black-footed albatross. The numbers in parentheses are sample sizes / number of breeding pairs.

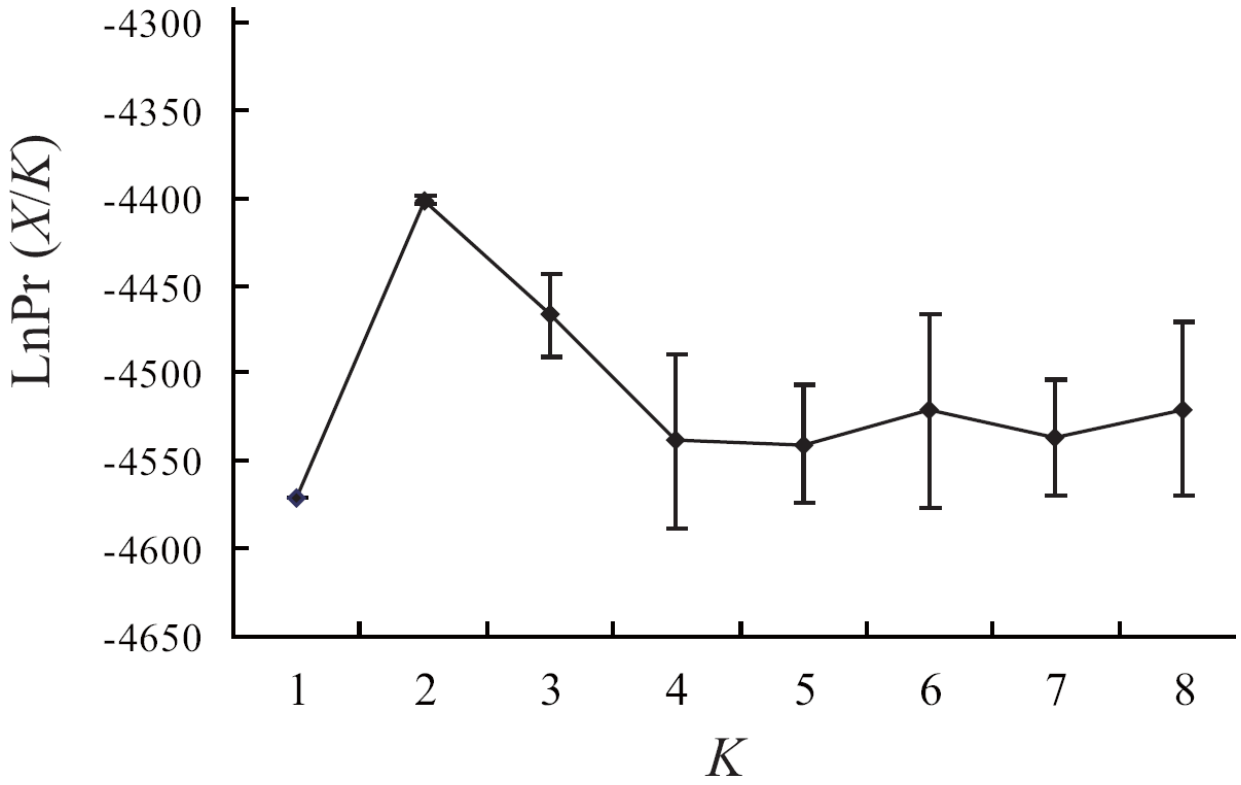
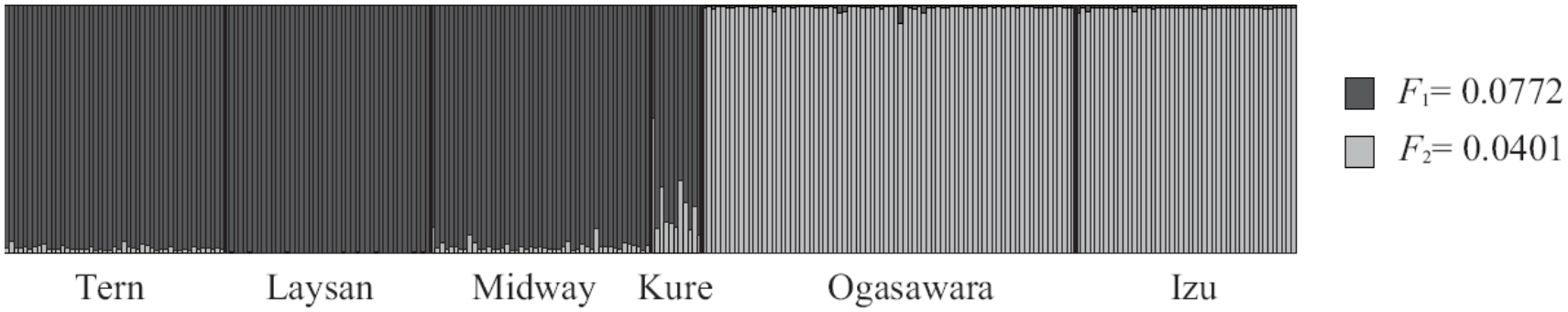


Fig. 2 Likelihood plot of STRUCTURE results. Ln Pr(X/K) is the log likelihood of each value of *K*, which is the number of simulated clusters. Where ln Pr(X/K) is maximized, *K* is most likely. Black squares represent the average values of ln Pr(X/K), and vertical lines represent standard deviations.

Fig. 3 Stacked bar chart from the results of STRUCTURE analysis with maximum likelihood *K*=2. Each individual is represented by a single bar, broken into *K* colored segments. The length of each segment is proportional to the membership fraction in each cluster. Individuals are grouped by population: Tern, Laysan, Midway and Kure in the central North Pacific and Ogasawara and Izu in the western North Pacific. The *F* values of each cluster are shown to the right.



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