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Conservation genetics and Pacific fisheries bycatch: Mitochondrial differentiation and population assignment in black-footed albatrosses (*Phoebastria nigripes*)

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Introduction

Recent population declines have coloured the demographies of many large pelagic seabird species. The largest of the seabirds are albatrosses (Procellariiformes: Diomedeidae) and most albatross species currently exhibit decreasing population numbers (Warham 1990; Gales 1998). Although the causes of their population declines are manifold (Gales 1998; Cousins and Cooper 2000), governments, scientists, and conservation agencies worldwide have established that incidental mortality (bycatch) of hundreds of thousands of seabirds annually in fisheries operations is an issue of international concern (Brothers et al. 1999; Stehn et al. 2001; Gilman and Freifeld 2003).

On the scale of whole oceans, an unambiguous means to identify region of origin (provenance) of bycatch birds would facilitate the identification of those regions most affected by bycatch mortality, especially since many seabird species show only minor morphological differentiation across their ranges (Mayr 1963; Waugh et al. 1999; Double et al. 2003). This information is necessary to assess the demographic impact to seabird populations of fisheries-induced mortality and to help guide both the development and the enforcement of fisheries regulations. An effective avenue to this end is to use DNA sequence data to evaluate the population genetic structure of the species in question, and to determine the percentage of the total bycatch that derives from each of its population isolates (Bowen et al. 1995; Edwards et al. 2001).

The black-footed albatross (*Phoebastria nigripes*) is one of three albatross species endemic to the North Pacific (Rice and Kenyon 1962; Fisher 1976; Warham 1991; Whittow 1993). As in other albatrosses, the life history of this species is characterized by delayed reproductive maturity (mode ~7 years; Cousins and Cooper 2000), long life expectancy (40 or more years), life-long pair bonding, and obligate biparental care of offspring. With the vast majority of pairs laying a single egg per year, their fecundity is low. Breeding occurs on remote islands, primarily in the Northwestern Hawaiian Islands where greater than 96% of the world's breeding population (~55,900 breeding pairs) is found, and in some smaller colonies more than 4000 km away, on islands off the main Japanese coast (~2000 breeding pairs; USFWS 2004; E. Flint personal communication; USFWS unpublished monitoring data). In 2003, black-footed albatrosses were listed as endangered by the World Conservation Union (Bird Life

International 2003). Mortality due to interaction with central North Pacific fisheries has been estimated conservatively at 1.9–5.0% of the global black-footed albatross population annually (Lewison and Crowder 2003), coincident with a substantial increase in fisheries operations around the Hawaiian Islands during the 1990s (Cousins and Cooper 2000). The primary objective of this study was to assess population genetic structure among colonies of black-footed albatrosses. These results were used as a basis for determining region of origin of 100 albatrosses killed incidentally in recent and historical fisheries.

Methods

Samples

Blood (~35–200 μl) or pin feather samples were collected non-destructively from black-footed albatrosses at colonies in the Northwestern Hawaiian Islands and Japan (Figure 1; Table 1). Samples were preserved in a lysis buffer or 95% ethanol and stored at −20 °C or at 4 °C. Sixty tissue specimens of black-footed albatrosses salvaged as bycatch from Japanese, Korean, and Taiwanese high seas squid and large-mesh driftnet fisheries in 1990 and 1991 (ranging between 29 and 45 °N and 148 and 153 °W; Ito et al. 1993) were obtained from the Burke Museum, University of Washington (museum accession numbers available upon request). Bycatch tissue specimens collected and archived under a cooperative venture of the USFWS, NOAA Fisheries Observer Program, and the University of Alaska Fairbanks (UAF) Museum in 2001 and 2002 were obtained from the UAF museum ($n = 6$). Bycatch samples from the 2002–2003 Hawaii-based fishery were obtained from the NOAA Fisheries Pacific Islands Region Hawaii Observer Program ($n = 21$). Bycatch samples from 2002 and 2003 British Columbia, Canada longline fisheries were obtained from the Canadian Wildlife Service ($n = 13$).

PCR amplification and sequencing

Genomic DNA was extracted either by a standard phenol: chloroform procedure (Sambrook et al. 1989) or using the Wizard® SV Genomic DNA Purification System (Promega, Madison, WI, USA). A 674 base pair (bp) fragment of mtDNA was amplified by the polymerase chain reaction (PCR) using primers L14863 (Nunn et al. 1996)

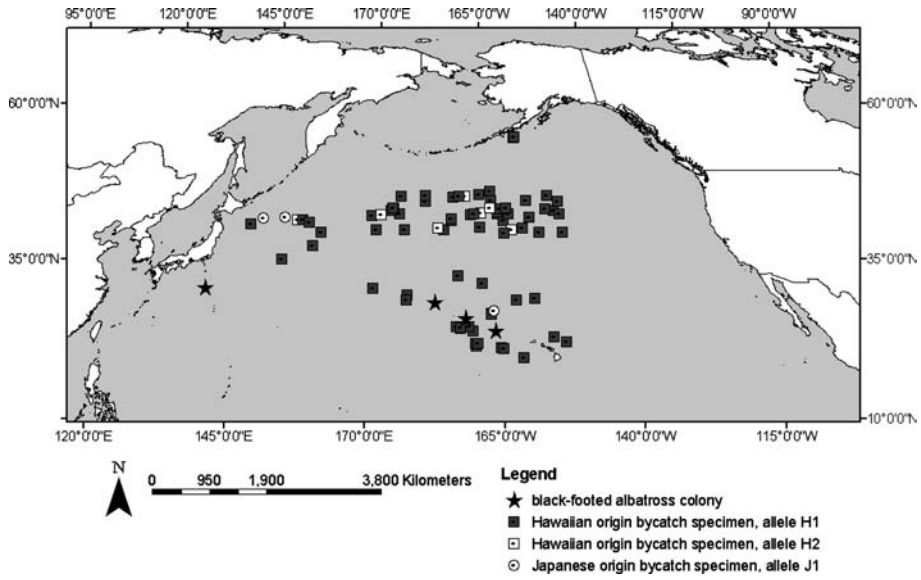

Figure 1. Bycatch sample distribution. Stars represent breeding colonies of Hawaiian and Japanese black-footed albatrosses, squares indicate collection localities of bycatch specimens assigned to Hawaiian origin, and circles indicate collection localities of bycatch specimens assigned to Japanese origin. Alternate alleles carried by the bycatch specimens are indicated as per the map legend. Bycatch samples from the BC, Canada fishery ($n = 13$, all Hawaiian origin) are not plotted because relevant coordinates for these samples are proprietary information.

Table 1. Polymorphic sites and frequencies of six haplotypes for the first 609 bp of the cytochrome *b* gene among black-footed albatross colonies

Haplotype	Polymorphic sites[a]								Haplotype frequency					
	S	S	S	S	S	S	S	N	French Frigate Shoals, Hawaii	Laysan Island, Hawaii	Midway Atoll, Hawaii	Hawaiian colonies overall	Izu Islands, Torishima, Japan	Total bycatch population
	3	3	4	4	4	5	5	5	23°45′N,	25°42′N,	28°12′N,		30°29′N,	
	0	2	0	1	8	4	4	8	166°15′W	171°44′W	177°20′W		140°18′E	
	0	7	2	1	9	0	6	1	(n = 46)	(n = 9)	(n = 30)	(n = 85)	(n = 55)	(n = 100)
H1	C	G	G	A	A	T	A	T	0.870	1.000	0.867	0.882	0.0182	0.87
H2	•	•	•	G	•	•	•	•	0.0435	0	0.0667	0.0471	0	0.09
H3	•	•	•	•	G	•	•	•	0.0217	0	0	0.0118	0	0.01
H4	T	A	A	•	•	•	G	C	0	0	0.0333	0.0118	0	0
H5	•	•	•	•	•	C	•	•	0.0435	0	0	0.0235	0	0
J1	•	A	A	•	•	•	G	C	0.0217	0	0.0333	0.0235	0.982	0.03

[a]S indicates a synonymous amino acid change, N indicates a non-synonymous (replacement) amino acid change; nucleotide positions are listed vertically and are relative to the first base of the gene; dot (•) indicates identity with the corresponding nucleotide in haplotype H1.

and H15487 (Bretagnolle et al. 1998), under conditions described in Walsh and Friesen (2003). PCR products were purified by PEG-precipitation (Sambrook et al. 1989) and used as template in 10 μl BigDye Terminator chemistry (version 1.1 or 3.1; Perkin-Elmer) cycle sequencing reactions. Sequencing reaction products were purified by alcohol precipitation and resolved by electrophoresis on an ABI PRISM™ 377 DNA Sequencer, or on a 3100 Genetic Analyzer capillary instrument (Applied Biosystems, Foster City, CA, USA). PCR fragments were sequenced in both forward and reverse directions. To check for amplification of nuclear homologs of this product, sequences derived from mitochondrial-only templates isolated from 30 tissue samples using the Wizard® *Plus* Minipreps DNA Purification System (Promega) were compared to those derived from whole genomic DNA. Chromatogram traces were basecalled using Phred (Ewing and Green 1998; Ewing et al. 1998), assembled (aligned) using PHRAP (Green 1994), and assemblies were visualized using CONSED (Gordon et al. 1998). Haplotype sequences have been deposited in the GenBank database under accession numbers AY641399–AY641404.

Analyses

Population genetic data analyses were performed using Arlequin ver. 2.000 (Schneider et al. 2000) and DnaSP ver. 4.0 (Rozas et al. 2003). Migration rates were estimated using MIGRATE ver. 1.7.3 (Beerli and Felsenstein 1999, 2001). Long-term female effective population size estimates (N_f) were derived from θ assuming a 1:1 sex ratio, an average generation time of 25 years (computed from life history data by Cousins and Cooper 2000), and a range of Kimura two-parameter (K2P; Kimura 1980) corrected divergence rates (2 μ) for cytochrome *b* (0.88–1.29%/MY; Nunn and Stanley 1998; 2%/MY; Avise and Walker 1998). Population divergence times (τ) were estimated as $\tau = D_A/2\mu$, where D_A is the net number of nucleotide differences between populations (Nei and Li 1979). The relative contributions of Hawaiian and Japanese populations to the total bycatch sample were evaluated using the maximum likelihood assignment software WHICHRUN ver. 4.1 (Banks and Eichert 2000).

Results

Nucleotide diversity and population structure

Sequence data revealed six haplotypes for a 609-bp fragment from the 5′ end of the cytochrome *b* gene (Table 1). As expected if the amplified sequences are truly mitochondrial in origin, sequences derived using both mitochondrial-only and genomic DNA templates were identical, and observed substitutions were concentrated at third codon positions. All of the observed substitutions were transitions, seven of which occurred at silent third codon positions and one of which occurred at a second codon position and caused a change between alanine and valine in the inferred amino acid sequence. Tests of neutrality indicated no deviations from neutral expectations for this locus [Tajima's (1989) $D = 0.96729$; Fu and Li's (1993) $D^* = -0.45587$; both $P > 0.10$]. Pairwise nucleotide diversity (π) was 3.2 times greater for the Hawaiian population than for the Japanese population, and corresponding female effective population sizes ranged from 4800 to 11000 and seven to 16 females, respectively.

AMOVA (Excoffier et al. 1992; Excoffier 2001) results revealed that 91.4% of the total genetic variation is distributed between Hawaii and Japan, that none of the total genetic variation is distributed among colonies within these regions and that 8.6% of the total genetic variation is distributed within colonies in these regions. Hawaiian and Japanese populations of black-footed albatrosses are significantly genetically differentiated ($\Phi_{ST} = 0.914$; $P < 0.0001$ by 1000 permutations). Pairwise Φ_{ST} values revealed no significant genetic structure among Hawaiian colonies for this locus (all $P > 0.47$). Exact tests of population differentiation (Raymond and Rousset 1995; Goudet et al. 1996) showed significant deviation from non-differentiation only for those pairwise comparisons of the Japanese population versus all other populations ($P < 0.0001$).

Gene flow

Female migration from Japan into any of the Hawaiian colonies, as estimated by the MIGRATE analysis, was negligible ($<10^{-10}$). Gene flow from the Hawaiian colonies as a whole into the Japanese population was

estimated at 5.8×10^{-3} (95% CI 9.9×10^{-4} –2.6×10^{-2}) migrants/generation. Among the four breeding colonies examined, migration rates greater than 10^{-10} were detected in only three of the 12 pairwise combinations of colonies: gene flow from Midway into French Frigate Shoals was estimated at 0.021 (0.015–0.029), from Laysan Island to Midway Atoll was 1.4×10^{-4} (7.7×10^{-5} –5.8×10^{-4}), and from Midway into Japan was 9.7×10^{-4} (2.4×10^{-4}–2.5×10^{-3}) (all units in migrants/generation).

Population history and divergence

D_A between the Hawaiian and the Japanese populations is 0.592%, which corresponds to a divergence time of not more than ~0.673–0.296 MYA (Edwards and Beerli 2000). Because population divergence estimates may be confounded by gene flow, we also estimated the K2P distance between the most common (i.e., likely the oldest; Watterson and Guess 1977; Crandall and Templeton 1993) Hawaiian haplotype and the most common Japanese haplotype. The distance between these common haplotypes is 0.66%, and they are estimated to have diverged from their common ancestral haplotype ~0.75–0.33 MYA.

Dynamics of bycatch birds

Because Hawaiian colonies of black-footed albatrosses formed a genetically homogeneous group for the cytochrome *b* data, WHICHRUN analyses were run with just two baseline populations (Hawaii and Japan). Three of the 100 bycatch individuals examined were identified as Japanese origin (Figure 1). Two of these individuals were collected in the 1990/1991 fishery and one was collected from the recent Hawaii-based fishery. The proportions of the bycatch sample that were of Hawaiian and of Japanese origins did not differ significantly from overall census proportions of Hawaiian versus Japanese birds for any of the four fisheries groups examined (Fisher's exact *P*-values all >0.25).

Discussion

Geographic differentiation and population histories

Efficient localization of wild individuals of uncertain provenance requires a level of differentiation between possible source populations (Wasser et al. 2004). In the present study, cytochrome *b* sequences revealed significant differentiation between Hawaiian and Japanese black-footed albatrosses. Negligible migration rates, coupled with size differences between Hawaiian and Japanese birds (Japanese birds being smaller; H. Hasegawa personal communication; Cousins and Cooper 2000) and other DNA differences between these groups (Edwards et al. 2001) suggest that these birds also may be reproductively isolated, despite overlap in their at-sea distributions. In the future, data from nuclear loci will help clarify the taxonomic status of these populations. The observed differences indicate a degree of independence of Hawaiian and Japanese black-footed albatrosses, and make these two groups (though evolutionarily young lineages) natural biological units for conservation and management purposes. The amount of cytochrome *b* sequence difference between Hawaiian and Japanese black-footed albatrosses is 0.59% [corrected (Nei and Li 1979); or 0.66% K2P distance, uncorrected for ancestral diversity] and is similar to that observed among taxa in the wandering albatross (*Diomedea exulans*) complex (0.52–0.87%, uncorrected; Penhallurick and Wink 2004), which have been described variously as separate species or subspecies (although not without controversy; Burg and Croxall 2004; Penhallurick and Wink 2004).

Effective versus census population sizes

The average value for the ratio of genetic effective population size to census size (N_e/N) of wild populations is 0.10–0.11 (Frankham 1995). Given that recent census data put the global estimates of breeding black-footed albatrosses at 55,886 breeding pairs in Hawaii, and 2021 pairs in Japan (USFWS 2004; E. Flint personal communication; USFWS unpublished monitoring data), the ratio of N_e/N is 0.086–0.20 for Hawaiian black-footed albatrosses and 0.0035–0.0079 for Japanese black-footed albatrosses, assuming a 1:1 sex ratio (0.050–0.25 and 0.0030–0.025, respectively, including 95% CIs for three divergence rate estimates). The fact that this ratio for the Hawaiian population is approximately equal to 0.10 indicates that the Hawaiian population harbors the level of cytochrome *b* variation expected for its size. However, the fact that the genetic effective size of

the Japanese population is up to 2 orders of magnitude lower than its observed census size suggests that this population has lost much genetic variation. For its census size, the Japanese population harbors a lower than expected degree of genetic variation (almost none), possibly due to the action of genetic drift in this small population (Wright 1969). The low genetic variability of the Japanese population may cause it consequently to suffer from inbreeding depression (e.g., Eldridge et al. 1999) and to be more vulnerable to extinction than the comparatively larger Hawaiian population. In terms of implications for potential redistributions of fishing effort, satellite telemetry studies of Japanese black-footed albatrosses would be invaluable for the identification of potential areas in which limiting fishing effort (e.g., time and area closures) may be effective for conservation of Japanese black-footed albatrosses.

Due to predominantly maternal transmission of mtDNA, the present data inform us only about population parameters for female black-footed albatrosses. Nuclear DNA data are required to evaluate whether or not significant genetic differentiation between Hawaiian and Japanese populations is a function of philopatry of both sexes. Given the uncertainty in reported divergence rate estimates for albatrosses (Nunn and Stanley 1998; Penhallurick and Wink 2004), increased accuracy of estimates of N_f and divergence times for black-footed albatrosses awaits more refined divergence rate estimates and inference based on a large number of unlinked loci from the nuclear genome.

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