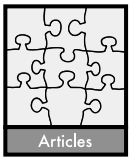

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Piecing together the global population puzzle of wandering albatrosses: genetic analysis of the Amsterdam albatross *Diomedea amsterdamensis*

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Wandering albatrosses have been subjected to numerous taxonomic revisions due to discoveries of new species, analyses of morphological data and, more recently, the inclusion of genetic data. The small population of albatrosses (170 individuals including 26 pairs breeding annually) on Amsterdam Island in the Indian Ocean, *Diomedea amsterdamensis*, has been given species status based on plumage and morphometrics, but genetic data published to date provide weak support and its specific status remains controversial for some authors. We used mitochondrial control region sequence data to elucidate the relationship of the Amsterdam albatross within the wandering albatross complex (*Diomedea amsterdamensis, D. antipodensis, D. dabbenena* and *D. exulans*). Three novel haplotypes were present in 35 individuals from Amsterdam Island, and were highly divergent (3.6–7.3%) from haplotypes found in the other three members of the wandering albatross complex. Low levels of genetic variation in Amsterdam albatross likely resulted, at least in part, from a population bottleneck. Geographic isolation in the wandering albatross complex is maintained by high natal philopatry. As Amsterdam Island is the only breeding ground for this critically endangered species, we strongly urge conservation efforts in the area, especially in relation to long line fisheries and other threats such as disease and introduced predators, and it be listed as a distinct species.

Albatrosses are wide-ranging, circumpolar seabirds and are mainly restricted to the southern hemisphere (Jouventin and Weimerskirch 1990, Prince et al. 1998, Nicholls et al. 2000, Nicholls et al. 2002, BirdLife International 2004, 2006). The high levels of natal philopatry and restricted number of breeding sites have had a profound effect on the levels of gene flow within this family of birds. Reproductive isolation due to natal philopatry, coupled with genetic drift from range expansion in the Pleistocene, has likely caused these taxa to become highly diverged (Burg and Croxall 2001, Abbott and Double 2003, Burg and Croxall 2004, Alderman et al. 2005, Bried et al. 2007, Milot et al. 2007).

Currently many discrepancies exist regarding the nomenclature of albatrosses (Nunn et al. 1996, Gales 1998, Brooke 2004). With respect to the wandering albatross complex there are four described species: *Diomedea amsterdamensis, D. antipodensis, D. dabbenena* and *D. exulans*. When it was first discovered in 1983, the distinct plumage, breeding phenology and morphology lead Roux et al. (1983) to describe birds on Amsterdam Island as a new species, *D. amsterdamensis*. However some researchers (Bourne 1989, Marchant and Higgins 1990, Warham 1990) continued to include the Amsterdam birds as a subspecies within the wandering albatross complex. Nunn and Stanley (1998) used cytochrome *b* (*cyt b*) to analyze relationships between Procellariiformes and found no fixed genetic differences between albatrosses on Amsterdam Island and *D. exulans*. However, *cyt b* may not be the optimal marker to detect genetic differences between populations as *cyt b* evolves more slowly, whereas, control region DNA is non-coding and evolves at a faster rate and, thus, is much more informative (Avise et al. 2000, Crochet et al. 2000, Milot et al. 2000, Burg and Croxall 2001, Wennerberg 2001).

Recent genetic studies have confirmed the distinctiveness of three species in the wandering albatross complex (Burg and Croxall 2004, Alderman et al. 2005, Milot et al. 2008). The most comprehensive study found three divergent groups: *Diomedea exulans* (Marion and Prince Edward, Crozet and South Georgia Islands), *D. antipodensis* (Campbell, Adams and Antipodes Islands off New Zealand), and *D. dabbenena* (Tristan da Cunha) (Fig. 1, Burg and Croxall 2004). Two subsequent studies found birds breeding on Macquarie and Kerguelen Islands belonged to the *D. exulans* group (Alderman et al. 2005, Bried et al. 2007). The genetics of the exulans group is well studied; however little population genetic data are available for breeding pairs on Amsterdam Island (Nunn et al. 1996, Milot et al. 2007). The most extensive study by Milot et al. (2007) compared two members of the complex and found reduced variation at nuclear loci

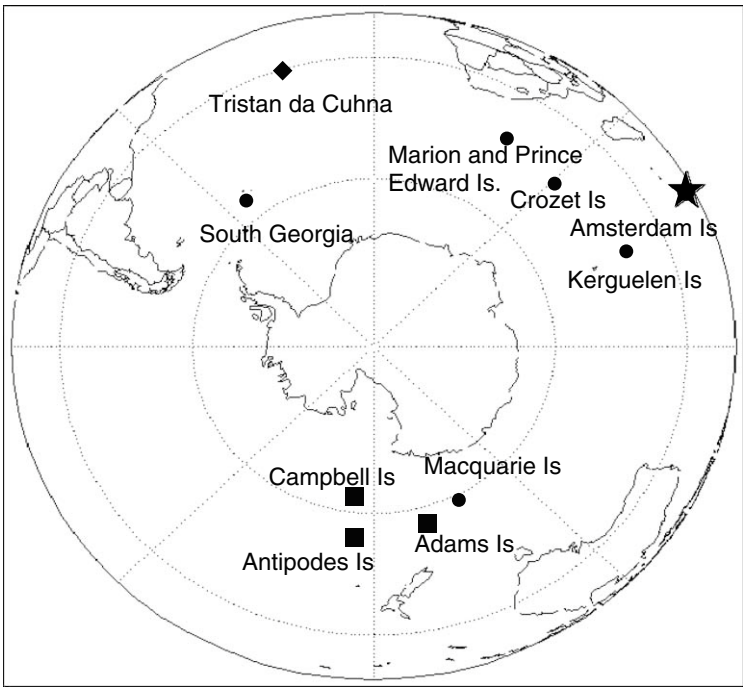

Figure 1. Breeding site distribution throughout the Southern Ocean for *Diomedea exulans* (circle), *D. dabbenena* (diamond), *D. antipodensis* (square) and *D. amsterdamensis* (star).

in *D. amsterdamensis* and genetic differences between *D. amsterdamensis* and *D. exulans*.

The aims of this study are to determine if the albatrosses breeding on Amsterdam Island form a genetically distinct group by assessing the levels of variation in the highly variable mitochondrial control region and to determine their relationship within the wandering albatross complex. Satellite telemetry studies on *D. amsterdamensis* show birds remain in the Indian Ocean and have specific foraging areas, but overlap with female and juvenile wandering albatrosses from the *D. exulans* group (Weimerskirch unpublished, Waugh and Weimerskirch 2003, Weimerskirch et al. 2006, Rivalan et al. 2010). Studies on other albatross species suggest that this may lead to a reduction in gene flow in some species (Burg and Croxall 2001, Burg and Croxall 2004, Friesen et al. 2007). The distinct dark plumage and smaller size of the Amsterdam birds would further suggest prolonged isolation (Roux et al. 1983, Cuthbert et al. 2003). Additionally, and importantly, philopatry likely plays a vital role in reducing gene flow between populations. Low levels of genetic variation are expected as the population on Amsterdam Island has probably suffered from a severe bottleneck with only five pairs in the early 1980s, when it was first discovered, and has increased gradually to only 26 breeding pairs annually (Weimerskirch et al. 1997, unpublished). Threats to the Amsterdam albatross include long line commercial fishing (Inchausti and Weimerskirch 2002), human commensals, such as rats and cats (Weimerskirch et al. 1997), and diseases (Weimerskirch 2004). This small population likely cannot withstand prolonged higher mortality rates from anthropogenic causes without expectations of extinction (Rivalan et al. 2010). We hypothesize that based on minimal overlap of foraging areas and the distinct plumage and morphometrics; the birds on Amsterdam Island will be distinct from the other three members of the wandering albatross complex.

Methods

Sampling, DNA extraction and amplification

Growing feathers were taken from a single chick at 35 nests prior to fledging on Amsterdam Island (137° 50′S 77° 35′E), kept in alcohol, and sent back to France for DNA extraction, originally for sexing as part of the demographic study. As Amsterdam albatross, and indeed all members of the wandering albatross complex, produce a single chick with each round of reproduction and successful birds breed every two years, the samples collected from chicks over the two summers (2002–2003) are not from siblings. DNA was extracted as directed by the manufacturer (Qiagen).

In many seabirds, including albatross, two copies of the control region are present in the mitochondrial genome (Abbott et al. 2005, Morris-Pocock et al. 2010, Eda et al. 2010). The two copies evolve in concert with the exception of the first ~100 bp. To assess the differences in the partial (F1) and complete (F2) copy of the control region, we sequenced both F1 and F2 copies from upwards of eight birds from Amsterdam (*D. amsterdamensis*) and four from Crozet (*D. exulans*). PCR reactions were carried out using H505 and specF2 or specF1 (see below, Abbott and Double 2003, Burg and Croxall 2004). Aligned sequences showed a similar pattern to that in other albatross species and boobies where F1 and F2 orthologs are more similar to each other within a species than homologs are (Supplemental Table 1). The first 102 bp are divergent, but the remaining portion of the sequence is highly conserved. Three of the previously published sequences are included for reference.

A 365 bp fragment of mtDNA CRD1 (control region domain 1) from the complete control region was amplified with 5 pmol of primers H505 (5'-GAAGAATGGTCCT GAAGC-3', Burg and Croxall 2001) and specF2 (5'-AAC AGCCTATGTGTTGATGT-3', Abbott et al. 2005) in 1.5 mM $MgCl_2$, 0.2 U *Taq* polymerase, 200 μM dNTP, and Thermopol II buffer (New England Biolabs). Thermal profile was one cycle of 120 s at 94°C, 45 s at 72°C and 120 s at 72°C; six cycles of 60 s at 94°C, 45 s at 50°C, 90 s at 72°C; 27 cycles of 60 s at 93°C, 30 s at 55°C, 60 s at 72°C; and a final cycle of 72°C for 5 min. All amplicons were visualized on a 1.0% agarose gel. Once amplified, amplicons were sequenced on an ABI 3730xl sequencer. Sequences were manually aligned using the program Se-Al CARBON v2.0a11 (Rambaut 2002). All nucleotide substitutions were confirmed by referencing the respective chromatogram.

To further investigate the global population structure of the wandering albatross complex we gathered all published mtDNA CRD1 haplotype sequences (Burg and Croxall 2004, Alderman et al. 2005) and aligned these with the new sequences.

Nested clade analysis

Nested clade analysis (NCA) was performed using TCS software v1.21 (Clement et al. 2000) to construct a statistical parsimony network at a 95% confidence interval. The network was produced in congruence with Steeves et al. (2005) with regards to breaking ambiguous branches. Clades were nested, as described in Templeton (1998), by starting at tips and moving toward the center to form *one-step clades*. *Two-step clades* were assembled using the previously made one-step clades as the basic groups to nest. Again, the minimal number of clades was grouped together from the tips toward the center. This was done until all haplotypes/clades were contained in one 5-step clade. Clades were statistically analyzed using the computer software GEODIS v2.5 to test interior to tip distances and the relationships between clades as a function of geographical distance (Posada et al. 2000).

Population structure analysis

AMOVA option in Arlequin v3.11 (Excoffier et al. 1992, 2005) was used to compute global F_{ST} and pairwise F_{ST} (100, 000 permutations), and MEGA3 was employed to calculate intra/inter population pairwise sequence divergences (Kumar et al. 2004). Analysis for isolation by distance (IBD) was done using GENEPOP v4.0 to correlate pairwise F_{ST} and pairwise distances (100, 000 permutations) (Raymond and Rousset 1995, Rousset 2008).

Results

MtDNA CRD1 sequencing found three haplotypes all of which were restricted to the Amsterdam albatross (R, S and T, see Supplemental Table 2) [sequences submitted to GenBank]. To address any concerns regarding sequence differences that may have resulted from accidental amplification of either the F1 or F2 copy of the control region in previously published sequences, we sequenced multiple *D. amsterdamensis* and *D. exulans* with the specF1/specF2 and H505 primer as above, for both F1 and F2 copies (Supplemental Tables 1 and 3). For all individuals the F1 and F2 copy from the same individual were identical for the portion of the control region reported in Supplemental Table 2, aside from the specF1/specF2 primer sequences. None of the sequenced Amsterdam albatrosses had a previously described haplotype from any species within wandering albatross species complex. Although there were three haplotypes on Amsterdam Island, the distribution was largely skewed. Haplotype R was present in 30 of 35 sampled birds (86%), while haplotypes S and T were present in 2 (6%) and 3 (9%) birds, respectively (Table 1).

Nested clade analysis

The nested clade analysis produced significant interior to tip distances at the 5-step clade and five lower level clades (Fig. 2). Significant clades were 2–3 ($\chi^2 = 22.86$, $p = 0.032$), 2–13 ($\chi^2 = 21.80$, $p = 0.038$), 3–5 ($\chi^2 = 10.65$, $p = 0.043$), 4–1 ($\chi^2 = 202.00$, $p < 0.001$), 4–2 ($\chi^2 = 21.00$, $p < 0.001$) and the entire cladogram ($\chi^2 = 73.434$, $p < 0.0001$).

Causal predictions of haplotype distribution and variation for significant clades were evaluated using the revised inference key along with GEODIS software as described by Templeton (2004). Clade 3–5 was statistically significant; however, the inference key lead to inconclusive results. The geographical distribution of clade 2–13 predicted that the clade had resulted from restricted gene flow. Clade 3–2 ($\chi^2 = 13.03$, $p = 0.065$) likely arose due to long distance colonization coupled with fragmentation or historical fragmentation followed by range expansion. Clade 4–1 was a result of allopatric fragmentation and the prediction for clade 4–2 is range expansion. The total cladogram was suggested to have arisen from historical fragmentation.

Population structure

High levels of population differentiation were found in the wandering albatross species complex ($F_{ST} = 0.806$, $p < 0.0001$). Pairwise F_{ST} ranged from -0.020 (treated as 0) to 0.954 (Table 2); however, overall they were high (average 0.618 ± 0.320). F_{ST} between the Amsterdam population and all other populations ranged from 0.819 to 0.954 (all significant at $p < 0.0001$). All significant values remained significant after sequential Bonferroni corrections (Rice 1989). Within group sequence divergence for *D. amsterdamensis* was 0.002 ± 0.001, *D. exulans* was 0.022 ± 0.001, *D. antipodensis* was 0.010 ± 0.003 and *D. dabbenena* was 0.000 ± 0.000). Between group sequence divergence ranged from 0.045 to 0.053 (see Table 3). Isolation by distance (IBD) analysis for all populations resulted in a positive, significant correlation between pairwise F_{ST} and geographic distance ($p = 0.011$). However, and despite being strongly influenced by the Amsterdam population; the pattern remains significant without the Amsterdam birds ($p = 0.028$).

Table 1. Geographical distribution of haplotypes is shown. New haplotypes are shown in bold. BI = Bird Island, South Georgia, Ma = Marion and Prince Edward Islands, Cr = Crozet Island, Mac = Macquarie Island, Ad = Adams Island, An = Antipodes Island, C = Campbell Island, Tr = Tristan da Cunha and Am = Amsterdam Island.

	D. exulans				*D. antipodensis*			*D. dabbenena*	*D. amsterdamensis*	Total
	BI	Ma	Cr	Mac	Ad	An	C	Tr	Am	
Unique	5	9	4	4	3	7	3			35
A	2									2
B			4							4
C	1	1	1							3
D	2									2
E		2	2							4
F					2					2
G						2				2
H					1	1				2
I						3				3
J					7					7
K						2				2
L					6	2				8
M					1		1			2
N						1	1			2
O								3		3
P				3						3
Q				2						2
R									**30**	30
S									**3**	3
T									**2**	2
Total	10	12	11	9	20	18	5	3	35	123

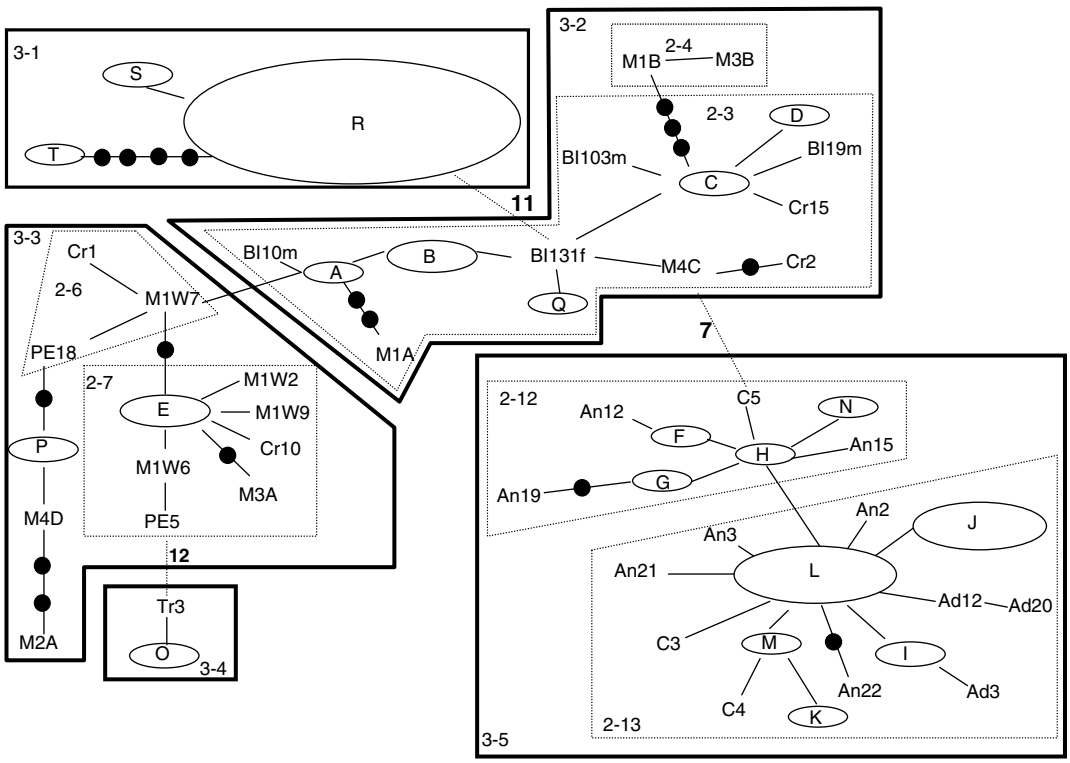

Figure 2. The cladogram based on 365 bp fragment of mtDNA control region representing all described haplotypes of all wandering albatrosses. Dark circles are inferred haplotypes and the three bolded numbers (7, 11 and 12) refer to the minimum number of steps between *D. exulans* and *D. antipodensis*, *D. amsterdamensis* and *D. exulans*, and *D. exulans* and *D. dabbenen*a, respectively. Two step clades are denoted by '2 —' and enclosed by a dotted line. Three step clades are denoted as '3 —' and enclosed by a bold line. The two four step clades (not shown) are clade 4–1 (clades 3–3 and 3–4) and clade 4–2 (clades 3–1, 3–2 and 3–5). Individual haplotypes are denoted as in Table 1 and Supplemental Table 2 and letters indicate a shared haplotype.

Table 2. Pairwise F_{ST} values are shown below the diagonal and corresponding P values are above the diagonal. Island abbreviations are given in Table 1. All significant values remain significant after Bonferroni correction to account for multiple pairwise tests. Bold F_{ST} values are significant.

	BI	Ma	Cr	Mac	Ad	An	C	Tr	Am
BI	–	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Ma	**0.144**	–	0.395	0.151	<0.001	<0.001	<0.001	<0.001	<0.001
Cr	**0.115**	0.026	–	0.118	<0.001	<0.001	<0.001	<0.001	<0.001
Mac	**0.298**	0.024	0.097	–	<0.001	<0.001	<0.001	<0.001	<0.001
Ad	**0.848**	**0.736**	**0.816**	**0.768**	–	<0.001	<0.001	<0.001	<0.001
An	**0.792**	**0.659**	**0.754**	**0.696**	**0.118**	–	0.868	<0.001	<0.001
C	**0.782**	**0.597**	**0.734**	**0.630**	**0.161**	−0.020	–	<0.001	<0.001
Tr	**0.823**	**0.569**	**0.760**	**0.637**	**0.872**	**0.824**	**0.824**	–	<0.001
Am	**0.905**	**0.819**	**0.884**	**0.843**	**0.923**	**0.898**	**0.930**	**0.954**	–

Discussion

MtDNA CRD1 sequencing yielded three haplotypes in the 35 Amsterdam albatross; none of these haplotypes are present in any other group. This, coupled with high F_{ST} values, suggests that the Amsterdam population is genetically distinct and has been isolated for a long period of time. Our data suggest the presence of a fourth distinct group, *D. amsterdamensis*, in the wandering albatross complex. Therefore this species complex contains no less than four lineages: (i) Tristan da Cunha, *D. dabbenena,* (ii) New Zealand, *D. antipodensis,* (iii) the widely distributed *D. exulans* and (iv) Amsterdam Island, *D. amsterdamensis*.

D. amsterdamensis is most genetically similar to *D. exulans*, the species with the nearest breeding site to Amsterdam Island at Kerguelen, 800 km apart. Within the wandering albatross complex, the strong IBD pattern indicates gene flow is restricted by geographic distance. However, the distribution of colonies and patterns of genetic variation suggest that other factors (e.g. natal philopatry, at-sea distribution) are maintaining genetic differences among the four groups. Each of the four groups has a relatively discrete foraging area during the breeding season, however there is important overlap between non-breeding birds and especially immature *D. exulans* and Amsterdam albatrosses (Prince et al. 1998, Weimerskirch 1998, BirdLife International 2004, Walker and Elliott 2006, Weimerskirch et al. 2006, Rivalan et al. 2010). Two of the four groups, *D. amsterdamensis* and *D. dabbenena*, have breeding sites to the north of the subantarctic front and these two islands groups, Tristan/Gough and St Paul's/Amsterdam, have a lot of similarities in terms of vegetation and avifauna. Rockhopper penguins north and south of the subantarctic front also exhibit reduced gene flow and have been divided into three species/subspecies (Jouventin et al. 2006, Baker et al. 2009) though there is evidence of dispersal (de Dinechin et al. 2007, Baker et al. 2009). Furthermore, in a pattern mirroring that of the wandering albatross complex, the rockhopper complex shows evidence of long term isolation in populations south of the subantarctic polar front including isolation of New Zealand rockhopper penguins from breeding sites in the southern Indian Ocean (e.g. Crozet) (Baker et al. 2009). Like the wandering albatrosses, rockhopper penguins have non-overlapping breeding distributions, but their distributions do overlap outside of the breeding season. The subantarctic and Antarctic fronts do not explain the reduced gene flow between *D. exulans* and *D. antipodensis*. The subantarctic *D. exulans* breeding on Macquarie Island are approximately 3500 km from the nearest breeding site of birds in the same group on Kerguelen, while they are only 700 km from the nearest *D. antipodensis* colony (Fig. 1). *D. antipodensis*, like *D. amsterdamensis* and *D. dabbenena*, overlap with *D. exulans* during the non-breeding season. Similarly, the vegetation and climate of the New Zealand islands are quite different from Macquarie and other *D. exulans* breeding sites.

Nested clade analysis of the geographic distribution of haplotypes suggests the wandering albatross complex is the result of allopatric fragmentation and this is further supported by the presence of four highly divergent groups. NCA predicted allopatric and historical fragmentation coupled with range expansion followed by restricted gene flow as speciation factors. Peripatric isolation of northern sites in the Atlantic and Indian Ocean, *D. dabbenena* and *D. amsterdamensis*, is evident. Assuming a 20%/MY mutation rate (Wenink et al. 1996, Baker and Marshall 1997), the species diverged approximately 225–265 kya. This is consistent with the notion that wandering albatross species emerged during the late Pleistocene and underwent a large, rapid range expansion followed by reproductive isolation (Alderman et al. 2005). Indeed other Southern Ocean species show similar patterns and/or timing of splits including other albatross (Burg and Croxall 2001, Abbott and Double 2003), white-chinned petrels (Techow et al. 2009), rockhopper penguins (Jouventin et al. 2006, de Dinechin et al. 2007, Baker et al. 2009) and intertidal kelp (Fraser et al. 2009). All of these studies show high levels of differentiation around New Zealand and those with species on Tristan/Gough show it is isolated from other breeding sites in the Atlantic Ocean. Fraser et al. (2009) sampled kelp at many of the same sites presented in this study and

Table 3. Between group sequence divergence (below the diagonal) and SE (above the diagonal).

	D. exulans	*D. antipodensis*	*D. dabbenena*	*D. amsterdamensis*
D. exulans		0.012	0.012	0.012
D. antipodensis	0.052		0.014	0.015
D. dabbenena	0.045	0.048		0.015
D. amsterdamensis	0.046	0.053	0.051	

interestingly found populations on islands from South Georgia east to Macquarie were relatively homogenous and distinct from those on Gough, Auckland, Campbell and Antipodes, among others.

Geographical distance between populations was shown to be a contributing factor to the global population structure as reflected by the positive correlation between F_{ST} and geographical distance. Interestingly within the most widespread group, *D. exulans,* no IBD was evident even over larger distances (Burg and Croxall 2004, Bried et al. 2007, Milot et al. 2007) though the number of known movements between archipelagos show more dispersal to nearby island groups than to distant sites (Bried et al. 2007, Milot et al. 2008). Given the wide distribution of albatrosses and their ability to disperse long distances (Jouventin and Weimerskirch 1990, Prince et al. 1998, Nicholls et al. 2000, Nicholls et al. 2002, BirdLife International 2004), high levels of gene flow between populations causing small F_{ST} values might be expected. However, strong natal philopatry and non-physical barriers (e.g. at-sea distribution) are restricting gene flow between populations. Wandering albatrosses are known to be highly philopatric (Inchausti and Weimerskirch 2002, Milot et al. 2008), and similarly there have been no recoveries of Amsterdam albatrosses on other Indian Ocean sites, or of other wandering albatrosses on Amsterdam Island, despite high recapture efforts on all Indian Ocean islands.

In conclusion, factors such as at-sea distribution and natal philopatry play an important role in speciation within the wandering albatross complex. We recommend that the population of albatrosses on Amsterdam Island be considered a distinct, evolutionarily important population for which a unique biological history exists and; in concert with morphological data, we ought to consider this population a distinct species, *Diomedea amsterdamensis*. Past studies (Burg and Croxall 2004, Alderman et al. 2005) coupled with our data suggest that restricted gene flow caused by natal philopatry leading to historical fragmentation has been the basis for four distinct lineages evolving within the wandering albatross complex.

Low levels of genetic variation in the Amsterdam albatross at both mitochondrial (this study) and nuclear loci (Milot et al. 2007) may not be solely the result of the strong bottleneck, but may be characteristic of wandering albatrosses in general (Milot et al. 2007). However, for Amsterdam albatrosses the extremely low genetic variation, even when compared to the other species in the complex, present conservation concerns. Only 170 Amsterdam albatross remain and all mature birds breed at a single site. The critically endangered Amsterdam albatross is threatened in large part by three issues. First, risks of accidental entanglement in long-line fishing gear (Inchausti and Weimerskirch 2002). Second, human commensals, such as cattle, cats and rats destroy nests and disturb breeding birds (Jouventin 1994). Recent fencing has protected the colony from trampling and habitat degradation by cattle. Cats can take young chicks, and rats and even mice may be a threat, although no observations have been made yet. On Gough Island mice attack and kill adult breeding Tristan albatrosses (Wanless et al. 2007). Finally, Amsterdam albatross lay a single egg every second year resulting in low reproductive output (Jouventin et al. 1989). While the current population appears to be stable, the low levels of genetic variation, small population size, non-genetic threats, and single breeding site put it at high risk of extinction.

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Supplemental Table 1. F1 F2 alignment. Numbers roughly correspond with Abbott et al. (2005) allowing for alignment between *Thalassarche* (*T. steadi*, Ste, *T. cauta*, Cau; *T. salvini*, Sal; *T. eremita*, Ere; and *T. bulleri*, Bul) and *Diomedea* (*D. exulans*, De;.*D. amsterdamensis*, Dam; *D. antipodensis*, Dan; and *D. dabbenena*, Dd). The last three sequences (De, Dan and Dd) are from Burg and Croxall (2004) with '?' indicating missing data due to the shorter sequence length. Section A in Abbott et al. (2005) corresponds to 1-102 below.

	Variable sites									
			111111	1111111111	1111111111	1112222222	2222222222	2222222222	2222222222	333
	11111222	3678888899	9999000111	1112222344	4566677777	7880000000	2222222344	4455557777	7888888899	022
	1623459678	0761235623	4789126246	7890359056	7056902347	8050123478	1234567034	7916791678	9123578939	949
SteF1	TTATAACCTC	ACCACTTGAA	CTGTAGGCCC	TCATATGAAA	TCCCATGCAT	AAGCTTCCAC	CTGCCATGTT	AGCTCGAACC	CGCATCTCCA	GCA
CauF1	G.........	......C..G	.......T..	....	C.....A...	...T.C....	....	....	....C.....	...
SalF1	....	......C...	.........T	.T........	......C..C	.....CT.GT	AC...CC...	...CT.....	....	.T.
EreF1	....	......C...	........TT	CT........	......CT..	...T.CT.GT	AC........	....	......CT..	.T.
BulF1	....	.T..T.C...	........TT	.T..C....G	...T..A..C	....C.T.GT	.CA.T.C.C.	GA..A..GA.	A.....CT..	...
DamF1	....	C.....C..G	A.A.C.A.A.	CT.C.CTCG.	.GATCCC...	TCTTC..TGA	..C.AC.C.C	GAACT.G..A	.CTCAACTT.	AT.
DeF1	....	C........G	A.A.CA.TAT	.T.C.CTCG.	..A.C.C...	TCTTC..TGA	..T.ACCC.C	GAACT.G..A	.CTCAACTT.	AT.
SteF2	ACG.TGTAA.	..T...CAG.	.C.C.A....	....	....	....	....	....	....	...
CauF2	GCGCT.TAAT	......CAG.	.C.C.A....	....	C.....A...	...T.C..GT	....	....	....C....G	...
SalF2	ACG.TGTAA.	...G...AG.	.CA..A...T	.T........	......C..C	.....CT.GT	AC...CC...	...CT.....	....	.T.
EreF2	ACG.TGTAA.	...G...AG.	.CA..A..TT	.T........	......CT..	...T.CT.GT	AC........	....	......CT..	.T.
BulF2	ACG.TGTAAT	...G.C.A.G	.C...A..TT	.T..C....G	...T..A..C	....C.T.GT	.CA.T.C.C.	GA..A...A.	A.....CT..	...
DamF2	ACG.TGT...	C.....C..G	A.A.C.A.A.	CT.C.CTCG.	.GATCCC...	TCTTC..TGA	..C.AC.C.C	GAACT.G..A	.CTCAACTT.	AT.
DeF2	ACG.TGT...	C........G	A.A.CA.TAT	.T.C.CTCG.	..A.C.C...	TCTTC..TGA	..TAACCC.C	GAACT.G..A	.CTCAACTT.	AT.
De	??????????	??????????	??????????	.TG..CTCG.	..A.C.C...	TCTTC..TGA	..TAACCC.C	GAACT.G..A	.CTCAACTT.	AT.
Dan	??????????	??????????	??????????	.TG..CTCG.	.GATCCC..C	TCTTC..TGA	.CCGACCC.C	GAACTTG..A	.CTCAACTT.	A.G
Dd	??????????	??????????	??????????	.TG..CTCG.	.GATC.CTCA	TCTTC..TGA	.CCAACCC.C	GAA.T.G..A	.CTCAACTT.	.T.

Supplemental Table 2. Variable site data for mtDNA CRD1 of wandering albatross species. All sequences are compared to 'BI10m' and similarities are denoted by '.'. Unique and shared haplotypes are listed as previously published and individual numbers for unique haplotypes are given in cases when the haplotype can be distinguished unambiguously (Burg and Croxall 2004, Alderman et al. 2005). New haplotypes described in this study are in bold.

	Variable sites				
	1111111111	1111111222	22222222222	2223333333	333333
	1344444577	7899999000	22234455555	8881134555	666677
	0406789434	9034589126	08917901258	4572773278	035605
BI10m	NNNTTGTCAG	CTAACCTCAT	AATTCCTTACC	CTGATACTAA	CGTCAA
Bl19m	....	....	.....T.C...	....	......
BI103m	....	..G.......	.....T.C...	.........G	......
Bl131f	....	....	.......C...	.........G	......
BI105f	....	....	.....T.C...	.........G	.A....
M1A	....	....	......CC..G	T.........	......
M1B	....	G.........	.....TCC.T.	T........G	......
M2A	....	....	.......C.T.	.....G....	.A....
M3A	....	....	..C........	T....G....	.A....
M3B	....	G.........	....TTCC.T.	T........G	......
M4C	....	....T.....	.......C...	....	......
M4D	....	....	........G..	.....G....	.A....
PE5	....	....	..C........	.........G	.A.T..
PE18	....	....	....	.C........	.A....
Cr1	....	....	....	Y.........	GA....
Cr2	....	....T.....	.......CG..	....	......
Cr10	....	....	..C........	....	.A....
Cr15	....	....	.....T.C...	.........G	....T.
MIW2	....	...C......	..C........	....	.A...N
MIW6	.....N....	....	..C........	....	.A.T..
MIW7	...NNN..G.	....	....	....	NNNNNN
MIW9	...NNN....	....	..C........	....	.A...T
Ad3	.....AC...	G...T....C	G.....CCG..	..T....CG.	.A.T..
Ad12	.....A....	G...T....C	......CCG..	..T....CG.	.A.T..
Ad20	.....A....	G...T....C	......CCG..	..T.C..CG.	.A.T..
An2	......Y...	G...T.C..C	......CCG..	..T....CG.	.A.T..
An3	....	G...T....C	.R....YCG..	..T....CG.	.A.T..
An12	....	G...T.....	......CCG..	..T.....G.	AA.T..
An15	....	G...T.....	......CCG..	..T....CG.	.ACT..
An19	....G.C...	G...T.....	......CCG..	..T....CG.	.T.T..
An21	......YT..	G...T....C	.G....CCG..	..T....CG.	.A.T..
An22	......YTG.	G...T....C	...C..CCG..	..T....CG.	.A.T..
C3	......Y...	G...TT...C	......CCG..	..TG...CG.	.A.T..
C4	....	G...T....Y	...C..C.G..	..T....CG.	.A.T..
C5	....	G...T.....	......CC...	..T....CG.	.A.T..
Tr3	....	G...T..TCA	......CC...	T....G....	.A....
A	......Y...	....	....	....	......
B	....	....	....	.........G	......
C	....	....	.....T.C...	.........G	......
D	.........A	....	.....T.C...	.........G	......
E	....	....	..C........	....	.A....
F	....	G...T.....	......CCG..	..T.....G.	.A.T..
G	....	G...T.....	......CCG..	..T....CG.	.T.T..
H	....	G...T.....	......CCG..	..T....CG.	.A.T..
I	....	G...T....C	G.....CCR..	..T....CG.	.A.T..
J	....	G...T..T.C	......CCG..	..T....CG.	.A.T..
K	.......T..	G...T....C	......C.G..	..T....CG.	.A.T..
L	....	G...T....C	......CCG..	..T....CG.	.A.T..
M	....	G...T....C	......C.G..	..T....CG.	.A.T..
N	....	G...T.C...	......CCG..	..T....CG.	.A.T..
O	......Y...	G...T..TCA	......CC...	T....G....	.A....
P	.....N....	....	........G..	T....G....	.A....
Q	...NNN..G.	.C........	......CC...	.........G	.....N
R	**CACCC.A...**	**G...T.C...**	**.......CCT.**	....	**.A....**
S	**GACCC.A...**	**G...T.C...**	**.......CCT.**	....	**.A....**
T	**CGTCC.A...**	**G...T.CT.C**	**......CCCT.**	....	**.A....**

Supplemental Table 3. F1 and F2 copies of control region. Samples were sequenced with specF1 or specF2 (denoted by F1 or F2 suffix). The non-conserved portion of the duplicated control region is located at the start of the sequence to site 48. DeBI10m is from Burg and Croxall (2004) where a shorter fragment was sequenced.

	Variable sites		
	111	1111111122	2222233
	3344448113	3444479900	5555836
	0513485041	4067995916	0125473
R	ACGTGTTCCG	ACCCAGTCCT	TCCTCAA
Dam1F2	....	....	....
Dam3F2	....	....	....
Dam5F2	....	....	....
Dam6F2	......G...	....	....
S	......GG..	....	......T
T	....	GT......TC	C......
Dam4F2	....	GT......TC	C......
Dam15F2	....	GT......TC	C......
Dam34F2	??????G...	....	....
DePB11F2	........TA	GTTTCCCT..	.TAC...
DePM14F2	.T......TA	.TTTTCCT..	.TGCTG.
Dam1F1	TTAAAC....	....	....
Dam3F1	TTAAAC....	....	....
Dam5F1	TTAAAC....	....	....
Dam6F1	TTAAAC....	....	....
Dam30F1	TTAAAC....	....	....
Dam33F1	TTAAAC....	....	....
Dam34F1	TTAAAC....	....	....
Dam4F1	TTAAAC....	GT......TC	C......
DePB11F1	TTAAAC..TA	GTTTCCCT..	.T.C...
DePM8F1	TTAAAC..TA	.TTTTCCC..	.T.C.GG
DePM9F1	TTAAAC....	....CCCT..	...C...
DePB10F1	TTAAAC....	....CCCT..	...C...
DeBI10m	??????????	??TTTCCT..	.TAC..G