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RESEARCH ARTICLE

Population genetic and behavioural variation of the two remaining colonies of Providence petrel (*Pterodroma solandri*)

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Abstract Knowledge of the dispersal capacity of species is crucial to assess their extinction risk, and to establish appropriate monitoring and management strategies. The Providence petrel (*Pterodroma solandri*) presently breeds only at Lord Howe Island (~32,000 breeding pairs) and Phillip Island-7 km south of Norfolk Island (~20 breeding pairs). A much larger colony previously existed on Norfolk Island (~1,000,000 breeding pairs) but was hunted to extinction in the 18th Century. Differences in time of return to nesting sites are presently observed between the two extant colonies. Information on whether the Phillip Island colony is a relict population from Norfolk Island, or a recent colonization from Lord Howe Island, is essential to assess long-term sustainability and conservation significance of this small colony. Here, we sequenced the mitochondrial cytochrome *b* gene and 14 nuclear introns, in addition to genotyping 10 microsatellite loci, to investigate connectivity of the two extant *P. solandri* populations. High gene flow between populations and recent colonization of Phillip Island (95 % HPD 56–200 ya) are inferred, which may delay or prevent the genetic differentiation of these insular populations. These results suggest high plasticity in behaviour in this species and imply limited genetic risks surrounding both the sustainability of the small Phillip Island colony, and a proposal for translocation of Lord Howe Island individuals to re-establish a colony on Norfolk Island.

Keywords Oceanic seabird · *Pterodroma solandri* · Gene flow · Behavioural variation · Conservation management

Introduction

Understanding mechanisms of population divergence has important implications for successful conservation of species (Avise 2000). While adaptation to different

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environments may be important for population persistence, it may also inhibit movements amongst populations, potentially reducing genetic variability through random genetic drift and inbreeding (Frankham 1996; Hedrick and Kalinowski 2000), which may decrease adaptability to future environmental variations (Frankham et al. 2002). Therefore, quantifying the dispersal of individuals, which is driven by the variability in intrinsic patch quality between different areas such as resource availability or population density (Bowler and Benton 2005), is essential to predict the long-term resilience and persistence of populations, and to inform management decisions such as supplementation and translocation (Frankham 1996).

Seabirds provide useful model systems for studying mechanisms of population divergence given their often philopatric behaviour and discrete breeding distributions (Friesen et al. 2007; Friesen 2015). Most oceanic seabirds breed in discrete colonies, and may constitute a population structure known as metapopulations, where occasional dispersal facilitates re-establishment or supplementation of populations following declines (Oro 2003). Nevertheless, the relative importance of the factors influencing dispersal between seabird colonies remains unclear (Friesen 2015; Welch et al. 2012). It is also crucial to identify factors influencing dispersal between seabird colonies to predict events such as genetic divergence or inbreeding depression (Avise 1996; Charlesworth and Charlesworth 1987). While physical barriers to dispersal and philopatry appear to be the main inhibitors of gene flow among seabird colonies (Friesen 2015; Warham 1990), other mechanisms have also been detected, such as differences in foraging distribution during the breeding and non-breeding seasons, differences in ocean regimes, and differences in breeding phenology (Burg and Croxall 2001; Friesen 2015; Wiley et al. 2012). For example, allochronic populations of band-rumped storm-petrel (*Oceanodroma castro*) appear genetically isolated in five archipelagos throughout the Atlantic and Pacific Oceans in the absence of physical barriers to gene flow (Smith and Friesen 2007). Conversely, whether genetic isolation exists among colonies that exhibit other phenological or circadian differences, e.g., diurnal versus nocturnal colony attendance has yet to be investigated.

The Providence petrel (*Pterodroma solandri*) is classified as vulnerable under both the *IUCN Red List of Threatened Animals* (Criteria D2) and the *New South Wales Threatened Species Conservation Act 1995* due to its restricted breeding range. The only significant breeding locality is Lord Howe Island (~32,000 breeding pairs) (Bester 2003), a small island located 600 km off the eastern coast of Australia (Fig. 1). Providence petrels previously bred on Norfolk Island (~1,000,000 breeding pairs), located approximately 1100 km northeast of Lord Howe Island (Fig. 1), before becoming extirpated following European settlement by the late 18th century (Medway 2002a). This species was considered extinct within the Norfolk Island group until 1986 when a small population (~20 breeding pairs) was discovered on Phillip Island, 7 km south of Norfolk Island (Hermes et al. 1986) (Fig. 1).

There is no evidence justifying taxonomic separation between Phillip Island and Lord Howe Island Providence petrels. However, it has been reported that Lord Howe Island individuals predominantly arrive at the colony during daylight (Bester et al. 2002; Medway 2002b), while Phillip Island individuals return to their breeding sites only after dusk (pers. obs.). This may relate to the presence of diurnal aerial predators—Brown Goshawks *Accipiter fasciatus*—at the time of European settlement on Norfolk Island (Medway 2002b), although no such predation risk presently exists. Alternatively, differences in foraging areas may explain time of return to colony (e.g., Dias et al. 2012). Given the possibility of selective significance, the observed difference in behaviour between colonies may inhibit gene flow between them.

Here we report a comprehensive study of the genetic distinctiveness between the two remaining breeding colonies of Providence petrel, to infer the dispersal patterns of this species and the conservation status of the small Phillip Island colony. We developed three genetic data sets, consisting of DNA sequences from mitochondrial and 14 nuclear regions and genotypes from 10 microsatellite loci, to investigate genetic connectivity and evolutionary history of Providence petrel colonies. Our study is also relevant to the proposed re-establishment of a colony on Norfolk Island using individuals from Lord Howe Island, with the aim of reducing the extinction risk of this species, and restoring the input of marine-derived nutrient into the ecosystem.

Materials and methods

Sample collection and DNA extraction

We collected blood samples from *P. solandri* individuals ($n = 151$) from four localities on Lord Howe Island (31°30′S, 159°05′E): Mount Gower (MG $n = 30$), Far Flats (FF $n = 79$), George's Bay (GB $n = 22$) and Muttonbird Point (MBP $n = 20$) (Fig. 1). We sampled the one locality on Phillip Island (29°12′S, 167°95′E) where the Providence petrel has been observed to nest: Jacky Jacky (JJ $n = 32$) (Fig. 1). All blood samples were collected from Providence petrels under Animal Ethics Permit number AEC 021028/02 issued by the Department of Environment, Climate Change and Water (NSW). Genomic DNA was extracted from 183 individuals using a Qiagen DNeasy® Blood and Tissue kit following the manufacturer's protocol.

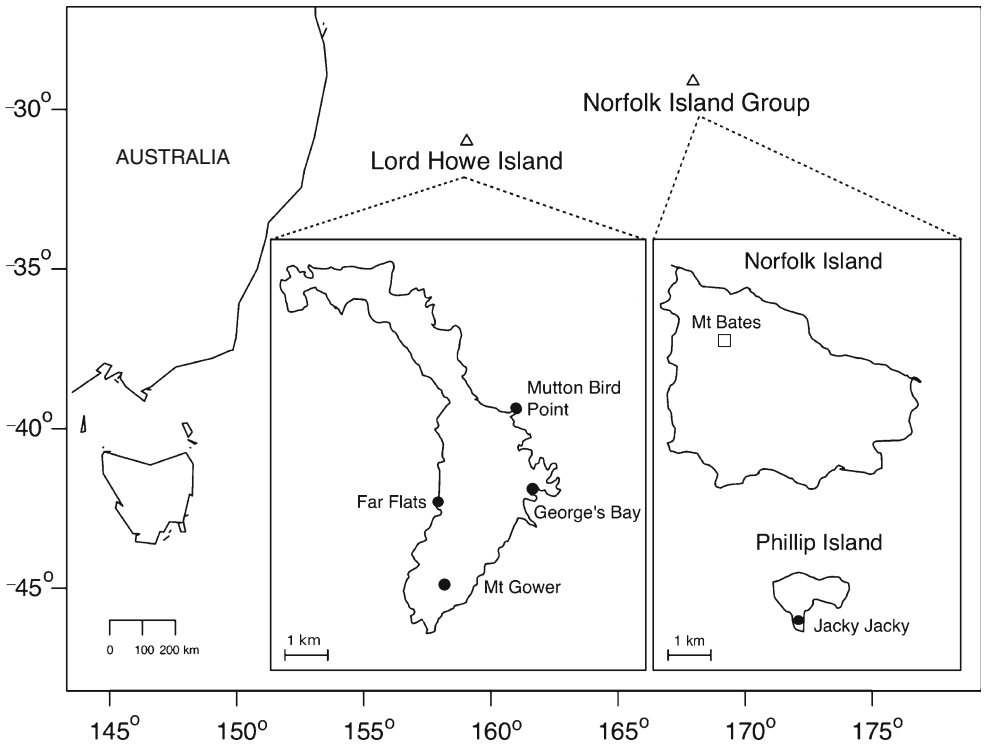

Fig. 1 Sampling locations for *Pterodroma solandri*. Lord Howe Island: Far Flats (FF, n = 79), George's Bay (GB, n = 22), Muttonbird Point (MBP, n = 20), Mount Gower (MG, n = 30). Phillip Island: Jacky Jacky (JJ, n = 32). Mount Bates was the location of the extinct Norfolk Island colony

Mitochondrial and nuclear DNA sequencing

We sequenced 183 individuals (151 from Lord Howe Island, 32 from Phillip Island) for a 872 bp fragment of the mitochondrial cytochrome *b* gene using primers L14841 (Kocher et al. 1989) and H15547 (Edwards et al. 1991). We also sequenced 40 individuals (20 from FF, Lord Howe Island, 20 from JJ, Phillip Island) for ~500 bp long fragments of 14 avian nuclear introns (Backström et al. 2008; Patterson et al. 2011; Silva et al. 2011). Primer sequences, optimal annealing temperatures and approximate locus length in *P. solandri* are shown in the electronic supplementary material, SI 1.

All fragments were PCR amplified with the MangoTaq™ DNA polymerase following the manufacturer's protocol (Bioline Inc.). PCR reactions were performed in 35 µL volumes using 50–100 ng DNA, and final concentrations of 0.5 U DNA polymerase, 0.2 mM of each dNTP, 1.5 mM $MgCl_2$ and 0.3 µM of each primer. The thermal cycling profiles included an initial denaturation at 95 °C for 1 min followed by 29 cycles of 95 °C for 30 s, 60–46 °C (decreasing the annealing temperature by 0.5 °C per cycle) for 40 s, and an extension of 72 °C for 90 s, with a final extension of 72 °C for 10 min followed by four similar cycles but with a constant annealing temperature at 45 °C. Negative controls were included with each set of PCRs.

Nucleotide sequences were determined on both strands of PCR products using a 3730xl DNA Analyzer (Applied Biosystem®) at Macrogen Inc., Korea. Sequences were aligned using the MUSCLE algorithm (Edgar 2004) in CODONCODE ALIGNER v3.7.1.1 (CodonCode Corporation). For sequences containing multiple heterozygous positions, we used the maximum likelihood method implemented in PHASE v2.2.1 (Stephens et al. 2001) to reconstruct the haplotype phase of the sequences. We conducted three independent runs of 10,000 iterations per locus with a different seed number to verify convergence, and discarded the first 1000 samples as burn-in. Phased haplotypes showing a probability >0.8 were used for further analyses.

Microsatellite genotyping

Genotypes of 183 individuals (151 from Lord Howe Island, 32 from Phillip Island) were determined at 10 polymorphic microsatellite loci (*Ptero9*, *Ptero7*, *Ptero6*, *Ptero4*, *Parm02*, *Parm03*, *Paequ 03*, *Paequ 13*, *Calex01*, *RBG29*) following Lombal et al. (2015).

Data analyses

Tests of assumptions and genetic variation

To assess levels of DNA sequence variation within colonies (Lord Howe Island, Phillip Island), haplotypic diversity *h* (Nei 1987), haplotype ratios X_H, nucleotide diversity π (Tajima 1983), and nucleotide diversity ratios π_R

(Mardulyn et al. 2009) were calculated for mitochondrial and nuclear intron DNA sequences with SPADS v 1.0 (Dellicour and Mardulyn 2014). To test whether patterns of genetic variation deviated from neutral expectations, Tajima's *D* test (Tajima 1983) and Fu and Li's *D** test (Fu and Li 1993) were performed using DNASP v 5.10 (Librado and Rozas 2009).

Microsatellite loci were tested for departure from Hardy–Weinberg equilibrium for each colony (Lord Howe Island, Phillip Island) using exact tests in ARLEQUIN v 3.5.1.2 (Excoffier and Lischer 2010), where Markov chain parameters were set at 10,000 dememorizations, and 10,000 iterations. The inbreeding coefficient F_{is} ($1–H_o/H_E$) was calculated per colony in FSTAT 2.9.2. (Goudet 1995), then tested for significant departure from zero using 10,000 permutations of alleles among individuals. Allelic diversity N_a, and allelic richness R_s, which uses a rarefaction method to standardize uneven sample size (Petit et al. 1998), were computed with the software HP-RARE v 1.0. (Kalinowski 2005).

Population connectivity and identification of dispersers

Estimates of pairwise population differentiation between Lord Howe Island and Phillip Island (F_{st}, G_{st}, N_{st} and Φ_{st}) were determined using SPADS v 1.0. (Dellicour and Mardulyn 2014). The statistical significance of F_{st}, G_{st}, N_{st} and Φ_{st} values was assessed by recalculating them based on 10,000 random permutations of individuals among islands. TCS networks (Clement et al. 2000) were inferred for mitochondrial and nuclear DNA sequences using PopART (http://popart.otago.ac.nz). AMOVA Φ-statistics (Φ_{SC} Φ_{ST} Φ_{CT}) (Excoffier et al. 1992) were calculated for the mitochondrial locus (cyt *b*) (Group 1 = JJ, Phillip Island; Group 2 = FF, MBP, MG, GB, Lord Howe Island) with 10,000 permutations of individuals and sampling sites. In addition, to evaluate the extent to which sequence variation was partitioned, a matrix of pairwise population differentiation was constructed between all sampling sites (n = 5).

F_{st} and R_{st} (Slatkin 1995) were calculated for microsatellites, the latter assuming a generalized stepwise mutation model (SMM), using FSTAT 2.9.2 (Goudet 1995), with significance assessed based on 10,000 permutations of alleles among samples. Contingency tables of alleles were generated, and classified (Kimura and Ohta 1978) using the log-likelihood statistic G (Goudet et al. 1996). G_{st} were not calculated for these high mutation rate markers as recommended by Whitlock (2011). AMOVA (Excoffier et al. 1992) was performed with 10,000 permutations of individuals among sampling sites (Group 1 = JJ, Phillip Island; Group 2 = FF, MBP, MG, GB, Lord Howe Island), and a pairwise population differentiation matrix was constructed among all sampling sites (n = 5) using GENODIVE v 2.0b28 (Meirmans and Van Tienderen 2004).

As low genetic divergence among populations could reflect high historical dispersal among populations that are now isolated, we used kinship-based methods to estimate current gene flow between *P. solandri* colonies (Lord Howe Island, Phillip Island), as recommended when there are low frequency alleles present (Hardy and Vekemans 2002). The statistical rigour and power of this approach using kinship coefficients (θ_{ij}) depends upon the overall level of genetic variation, and not the degree of divergence between populations (Palsboll et al. 2010). We calculated θ_{ij} (Loiselle et al. 1995) for each pair of individuals in GENODIVE (Meirmans and Van Tienderen 2004). To test whether individuals collected in the same colony were more closely related to each other than individuals collected in different colonies, we performed a non-parametric Permutational Multivariate Analysis of Variance (PERMANOVA) on θ_{ij}. This approach partitions the distance matrix according to the source of variation (e.g., among vs. within), and compares the sum of square distances among and within these groups as implemented in PERMANOVA + 1.0.6 software add-on running on PRIMER6 (Clarke and Warwick 2005). To assign θ_{ij} to independent genetic clusters, we used a *K*-Means method to calculate the Calinski-Harabasz pseudo *F*-statistics (Caliński and Harabasz 1974), which focuses on reducing the within-group sum of squares, for $K = 2–183$, with 10,000 iterations per cluster, as implemented in the package *clusterSim* in R v 3.2.1.

Bayesian clustering analysis and individual assignment

Bayesian clustering analysis, which uses MCMC simulation to assign coancestry of individuals to independent genetic clusters (*K*) based on individual microsatellite genotypes without a priori assumptions of populations, was implemented in STRUCTURE v 2.3.3 (Falush et al. 2003; Pritchard et al. 2000). Exploratory runs showed that a burn-in of 200,000 followed by 1,000,000 iterations achieved stable estimates. 20 replicate runs were then performed for all values of $K = 1–8$, reflecting the highest expected number of genetic cluster ($n = 5$, Far Flats (FF), Mount Gower (MG), George's Bay (GB), Muttonbird Point (MP), and Jacky Jacky (JJ)) plus three (Evanno et al. 2005). We used the admixture model, and assumed correlated allele frequencies, which is expected to perform better when genetic structure is weak or when the number of loci is <20 (Hubisz et al. 2009), with Prior Mean = 0.01, and Prior SD = 0.05. We implemented priors for alpha ($\alpha = 1$) and lambda ($\lambda = 1$), specifying the degree of admixture between populations and the distribution of allele frequencies respectively, for all populations. The optimal

number of clusters (K) was estimated by calculating the second order-rate of change (ΔK) of the likelihood function (ln $P(X/K)$) with respect to each K (Evanno et al. 2005), as implemented in the program STRUCTURE HARVESTER (Earl 2012). The results of all runs were summarized in CLUMPP v 1.1.1 (Jakobsson and Rosenberg 2007) using the *FullSearch* algorithm, and then visualized using DISTRUCT v 1.1 (Rosenberg 2004).

Migrant individuals between colonies (Lord Howe Island, Phillip Island) were identified using exclusion methods as implemented in GENECLASS 2.0 (Piry et al. 2004). We used the exclusion criterion L_h/L_{max} (Paetkau et al. 2004) to compute the probability that an individual belongs to a colony. We compared the Bayesian (Rannala and Mountain 1997) and frequency based criteria (Paetkau et al. 2004) to calculate the likelihood of individual origin. We used the Paetkau et al. (2004) resampling methods based on allele frequency (Paetkau et al. 2004), which demonstrated low type I error rates (1 % of the number of individuals per population that appear to be immigrants by chance). This method generates population samples of the same size as the reference population sample, as recommended for detection of first generation migrants (Piry et al. 2004). The marginal probability of given individual multilocus genotype was compared to the distribution of marginal probabilities of randomly generated multilocus genotypes (100,000 replicates) with a type I error threshold setting at $\alpha_{0.01}$ and $\alpha_{0.05}$.

Estimation of divergence time

We used IMa and its model of isolation with migration (Hey and Nielsen 2007) to simultaneously estimate migration (m_1, m_2) and lineage divergence time (t) between *P. solandri* colonies (Lord Howe Island, Phillip Island). This coalescent-based model is based on several assumptions including neutrality, random mating in ancestral and descendent populations, and free recombination between loci, but none within loci (Hey and Nielsen 2004; Nielsen and Wakeley 2001). Lack of recombination within nuclear introns was tested using the four-gamete test as described by Hudson and Kaplan (1985), and loci suspected to be under selection were excluded from analyses (Supplementary Material, SI 3). An IMa exploratory run was performed to assess a range of prior distributions that include most of the range over which the posterior density is not trivial. Analyses were then run three times with different seed numbers to test for convergence, with 10,000,000 sampled steps following a discarded burn-in of 200,000 steps, with a two-step linear heating scheme with five chains. We implemented the Hasegawa-Kishino-Yano (HKY) (Hasegawa et al. 1985) model for the mitochondrial data, the infinite sites mutation model (IS) (Kimura 1969) for the nuclear introns, and the Stepwise Mutation Model (SMM) (Kimura and Ohta 1978) for microsatellites. Mutation rates were given as priors to the analysis with $\mu = 1.89 \times 10^{-8}$ and 3.6×10^{-9} substitution/site/year for cyt *b* and nuclear introns respectively, as recommended for other seabirds (Axelsson et al. 2004; Weir and Schluter 2008), and $\mu = 5 \times 10^{-4}$ substitution/site/year for microsatellites (Brown et al. 2010). To assess the estimates of demographic parameters, we used a generation time $T = 10$ years, as calculated based on the following equation $T = A + p/(1-p)$ (Sæther et al. 2004), with p the adult survival rate ($p = 0.82$) (Brooke 2004), and A the age of sexual maturity ($A = 6$ years) (Warham 1990). Parameter trend line plots and values of effective sample sizes (ESS) were inspected after each run.

Demographic history

Historical demographic changes in the only significant colony of Providence petrels (Lord Howe Island) were inferred from two complimentary coalescent modeling approaches of microsatellite data using MSVAR v0.4 (Beaumont 1999) and MSVAR v1.3 (Storz and Beaumont 2002). This approach is more robust than classic methods based on summary statistics to detect changes in population size (Girod et al. 2011).

MsVar v0.4 inferred the magnitude of change in population size ($r = N_0/N_1$, where N_0 and N_1 are current and ancestral population sizes, respectively) assuming a SMM model for the microsatellite loci. We initially conducted three independent simulations varying the prior distributions to examine their effect on the posterior distribution. We then ran the simulation three times under the exponential and the linear model, with different seed numbers for each dataset, for 4×10^9 iterations with parameter values recorded every 1×10^5 iterations, resulting in 40,000 records. We discarded 10 % of recorded values for each chain (i.e., burn-in), and we performed the Brooks, Gelman and Rubin Convergence diagnostic tests (Gelman and Rubin 1992) as implemented in the package BOA (Smith 2007) for R version 3.2.1. (Venables and Smith 2001). We considered that chains converged well when values lower than 1.1 were obtained. The chains were then combined to estimate the 90 % high probability density (HPD) of demographic parameters using the package CODA as implemented in R (Plummer et al. 2006). The strength of evidence for population increase versus decrease was evaluated by calculating the Bayes factor of each of the simulations (Girod et al. 2011; Storz et al. 2002). This ratio can be estimated by counting the number of states in the chains in which the population has decreased (i.e., $N_0/N_1 < 1$), and then dividing this by the number of states in which the population has increased

(i.e., $N_0/N_1 > 1$) with BF 0–3 no support of contraction, 3–10 substantial support, >10 strong support (Storz and Beaumont 2002).

Msvar 1.3 was used to quantify population sizes and time of change. MsVar 1.3 uses probable genealogies of allele frequency data to generate posterior probability distributions of four natural demographic parameters, $\Phi = N_0, N_1, ta,$ and $\theta,$ where N_0 and N_1 are the current and the ancestral effective population size respectively, *ta* is the time since the demographic changes began, and $\theta = 4N_0\mu$, the rate of mutation scaled by population size. This model differs from the previous model in that all loci are used in the same MCMC simulation, reducing density estimation error, and that all parameters are free to vary among loci. We inferred broad normal distribution priors and hyper-priors (Supplementary material, SI 2), and we ran the simulation three times under the exponential model to evaluate recent changes in population size ($\log_{10}(T) < 10$). MCMC chain convergence, 90 % HPD of posterior distributions and Bayes factors were inferred as described for Msvar v0.4.

Results

We sequenced 872 bp of the mtDNA cytochrome *b* gene in 151 and 32 individuals from Lord Howe Island and Phillip Island, respectively, and a total of 7837 bp comprising 14 nuclear introns in 20 individuals from both colonies, defining 2–9 (Phillip Island) and 1–17 (Lord Howe Island) alleles (Supplementary Material SI 3). No significant difference in nucleotide diversities (π) between colonies was detected (One-way ANOVA; H_0 = means of π_R are equal in Lord Howe Island and Phillip Island, where π_R represents the nucleotide ratio; $F = 0.91$; p value = 0.349; see π_R values in Supplementary Material SI 3). Tajima's *D* statistics showed significant negative values in the mitochondrial locus (*cyt b*, $D = -1.987$, $p < 0.05$), and in one nuclear intron (*δ-cryst*, $D = -2.030$, $p < 0.05$) for Lord Howe Island and Phillip Island populations respectively, while Fu and Li's *D** tests showed negative values for two loci (*cyt b*, $D^* = -2.920$, $p < 0.05$, and *16214*, $D^* = -3.110$, $p < 0.05$) for Lord Howe Island, and in one locus (*Pema05*, $D^* = -2.167$, $p < 0.05$) for Phillip Island (Supplementary Material SI 3).

Ten microsatellite loci were genotyped in 151 and 32 individuals from Lord Howe Island and Phillip Island, defining 2–51 and 4–30 alleles per locus, respectively. No significant difference in genetic diversity between populations was detected (Kruskal–Wallis test; H_0 = means of R_s are equal in Lord Howe Island and Phillip Island, where R_s represents allelic richness; $F = 1.12$; p-value = 0.289; see R_s values in Table 1), and no significantly positive values of F_{is} were found for either Lord Howe Island or Phillip Island (Table 1).

Population connectivity

Visual inspection of haplotype networks (Fig. 2, Supporting Material SI 4), observation of low *F*-statistics (global $F_{st} = 0.004$, $p > 0.05$; global $G_{st} = 0.004$, $p > 0.05$, Table 2) and lack of significant phylogeographic signals (global $\Phi_{st} = 0.019$, $p > 0.05$, global $N_{st} = 0.033$, $p > 0.05$, Table 2) indicate no genetic differentiation between Lord Howe Island and Phillip Island. AMOVA Φ-statistics showed no differentiation between sampling locations or group of sampling locations for cyt *b* (Group 1 = JJ, Phillip Island; Group 2 = FF, MBP, MG, GB, Lord Howe Island; $\Phi_{SC} = 0.0004$, $p > 0.05$; $\Phi_{ST} = 0.016$, $p > 0.05$; $\Phi_{CT} = 0.016$, $p > 0.05$), and the F_{st} pairwise matrix showed no significant genetic structure between pairs of *P. solandri* sampling sites (Table 3). F_{st}, R_{st} and AMOVA *F*-statistics obtained with microsatellites were not significantly different from zero between Phillip Island and Lord Howe Island sampling locations (global $F_{st} = 0.006$, $p > 0.05$; global $R_{st} = 0.004$, $p > 0.05$, Table 1). Pairwise F_{st} indicated no genetic differentiation between *P. solandri* sampling sites (Table 3). These results refute structuring of genetic variation between Lord Howe Island and Phillip Island.

Kinship coefficients (θ_{ij}) ranged from −0.28 to 0.69 and −0.27 to 0.36 within and between colonies, respectively. The analysis of variance of θ_{ij} showed no significant differences between 'within-colonies' and 'among-colonies' (pseudo-$F_{1,182} = 0.993$, $P = 0.424$). The clustering analysis, based on Calinski-Harabasz pseudo-*F* statistics, showed highest pseudo-*F* for $K \gg 2$ (Fig. 3), which does not support Phillip Island and Lord Howe Island as genetically distinct colonies.

Bayesian clustering analysis and individual assignment

Evaluation of lnP(*X*/*K*), Δ*K*, and Q obtained with STRUCTURE supported $K = 4$, although genetic clusters did not reflect geographical localities. Each individual contained roughly equal coancestry from the four clusters (Supplementary material SI 5). The frequency-based and Bayesian assignment methods (Lord Howe Island vs. Phillip Island colonies) implemented in GENECLASS 2 showed 3 and 7 ($\alpha_{0.01}$), and 12 and 23 ($\alpha_{0.05}$) first-generation migrants, respectively (Supplementary Material SI 6). Conversely, the two methods showed equivalent results with 59 % of individuals correctly assigned (108 out of

Table 1 Characterization of genetic diversity and summary statistics in *P. solandri* for 10 microsatellites loci

Locus name	Length (bp)	Lord Howe Island (n = 151)					Phillip Island (n = 32)					All populations		
		A	R_s	H_0	H_e	F_{is}	A	R_s	H_0	H_e	F_{is}	F_{st}	R_{st}	F_{is}
Ptero09	187–235	17	14.47	0.671	0.879	0.234	13	10.93	0.688	0.886	0.227	−0.004	0.024	0.232
Ptero07	264–344	51	41.26	0.968	0.954	−0.008	30	21.25	1.000	0.972	−0.029	−0.007	0.002	−0.010
Parm03	177–181	6	5.00	0.654	0.663	0.011	4	3.75	0.469	0.637	0.268	0.004	0.024	0.055
Ptero06	141–149	2	2.00	0.033	0.185	0.821	3	2.94	0.156	0.347	0.553	0.038	−0.016	0.746
PaEquation 13	146–148	5	4.20	0.266	0.352	0.239	4	3.023	0.355	0.421	0.159	0.006	0.004	0.222
Calex01	237–255	14	13.75	0.859	0.859	−0.002	13	11.33	0.938	0.892	−0.052	0.008	−0.006	−0.011
Ptero04	150–168	11	10.45	0.821	0.826	0.006	10	8.22	0.906	0.812	−0.119	−0.003	0.021	−0.016
RBG29	124–136	9	7.51	0.653	0.805	0.215	6	5.90	0.813	0.796	−0.021	−0.014	−0.010	0.181
Parm02	192–198	6	5.00	0.415	0.411	0.003	5	4.20	0.375	0.489	0.235	0.006	−0.009	0.049
PaEquation 03	222–232	10	8.88	0.614	0.678	0.038	8	6.94	0.844	0.827	−0.020	0.019	−0.004	0.030

Allelic diversity *A*; allelic richness R_s; and tests for departure from Hardy–Weinberg equilibrium. Inbreeding coefficient F_{is} $(1-H_o/H_E)$. Population structuring (F_{st} and R_{st})

All *p*-values > 0.05

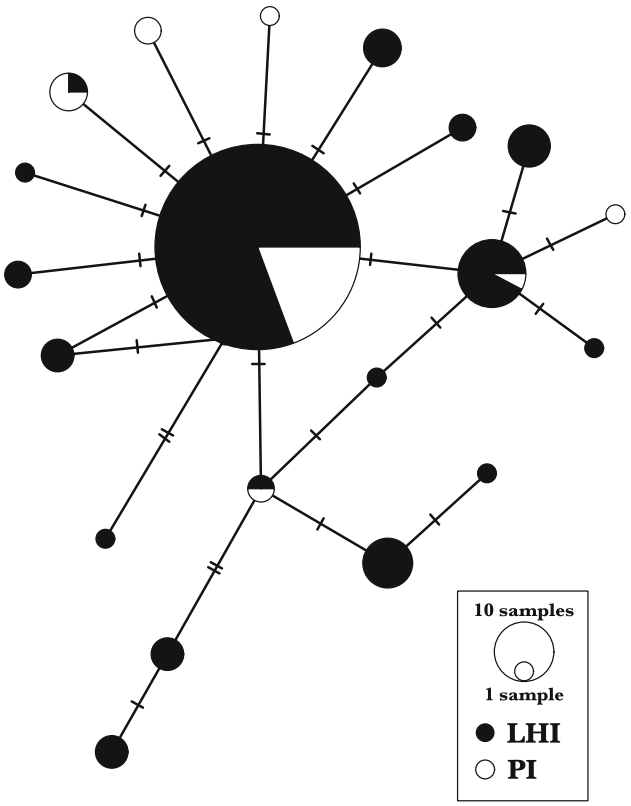

Fig. 2 Haplotype network of Providence petrel (*Pterodroma solandri*) mtDNA haplotypes based on the TCS algorithm. Haplotypes are represented by *circles*, where the size of each *circle* is proportional to the frequency of the corresponding haplotype. *Lines* on connecting branches represent mutations. *Black*: Lord Howe Island individuals. *White* Phillip Island individuals

183) with an average probability of 54.28 % at $\alpha_{0.05}$, and 53.39 % at $\alpha_{0.01}$. This low confidence reflects the similarity between likelihoods of genotypes across populations.

Table 2 Summary statistics in *P. solandri* for the mitochondrial *Cytochrome b* gene and 14 nuclear introns

Locus name	F_{st}	Φ_{st}	G_{st}	N_{st}
Cyt b	0.0105	0.1050	0.0061	0.0200
δ-cryst	0.0810	0.0810	0.0283	0.0810
Lipo2	0.0000	0.0000	0.0000	0.0000
Pema01	−0.0014	−0.0014	−0.0119	−0.0014
Pema05	0.0256	0.0256	0.0141	0.0256
Pema07	−0.0006	−0.0006	0.0135	0.0058
Pema10	0.0148	0.0148	0.0260	0.0148
Pema12	−0.0148	−0.0148	−0.0102	−0.0148
Pema13	−0.0129	−0.0129	−0.0208	−0.0129
Pema14	0.0203	0.0203	0.0130	0.0203
16214	−0.0002	−0.0002	−0.0117	−0.0002
20454	0.0166	0.0166	−0.0050	0.0166
22519	−0.0037	−0.0037	−0.0027	−0.0037
24206	−0.0221	−0.0221	−0.0197	−0.0221
24972	0.0170	0.0170	0.0178	0.0170

Pairwise population differentiation between Lord Howe Island and Phillip Island colonies, F_{st}, G_{st}, N_{st} and Φ_{st}, where Φ_{st} represents the direct analog of Wright's F_{st} for nucleotide sequence diversity (Excoffier et al. 1992)

All *p*-values > 0.05

Estimation of divergence time

Implementations of the isolation-with-migration model using microsatellites, nuclear introns and mitochondrial loci resulted in unimodal posterior density curves of migration parameters, which were similar across the three

Table 3 Pairwise differentiation matrix among *P. solandri* colonies

	JJ	FF	MBP	GB	MG
JJ	–	0.022	−0.003	0.042	0.022
FF	0.005	–	0.003	0.004	−0.017
MBP	−0.010	0.012	–	0.058	0.002
GB	−0.004	0.002	0.000	–	−0.002
MG	−0.003	0.003	0.004	−0.010	–

F_{st} among *Pterodroma solandri*. Lord Howe Island: Far Flats *FF*; George's Bay *GB*; Muttonbird Point *MBP*; Mount Gower *MG*; Phillip Island: Jacky Jacky *JJ*; Above diagonal: pairwise differentiation matrix for mitochondrial DNA. Below diagonal: pairwise differentiation matrix for 10 microsatellites

All p-values > 0.05

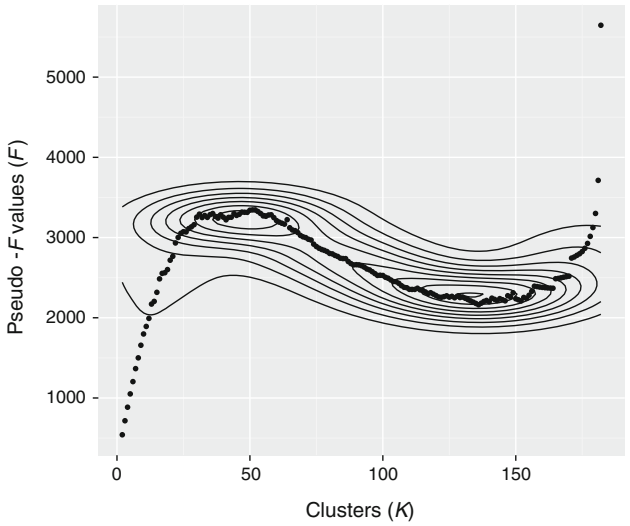

Fig. 3 Calinski-Harabasz pseudo F-statistic density for kinship coefficients (K = 2–183). Highest density of pseudo-F-statistic values determine the most likely number of clusters among *P. solandri* individuals

runs. Migration rates were of 0.32 migrants/generation from the Phillip Island colony to the Lord Howe Island colony (0.24–0.49 90 % HPD) (Fig. 4a), and 8.6 migrants/generation from the Lord Howe Island colony to the Phillip Island colony (8.44–8.73 90 % HPD) (Fig. 4b). Divergence time estimates were also convergent across all analyses, corresponding to 88 years (56–200 90 % HPD) (Fig. 4c).

Demographic history

Results from coalescent modelling of microsatellites using MsVar v0.4 and Msvar 1.3 both showed a strong signal for large population decrease in the Lord Howe Island colony (Fig. 5a, b). Combining all simulations for all datasets, contemporary effective population size, N_0 (30 [0–1862], mean and 90 % HPD) was three orders of magnitude smaller than the ancestral effective population size, N_1 (177,827 [5888–4,265,795], mean and 90 % HPD) (Fig. 5b). All Bayes factors obtained with both methods were $\gg 10$ in favour of population decrease rather than increase. The time when the ancestral Lord Howe Island colony started to decrease (mean $\log_{10}(t_f) = 2.785$, exponential model) suggests a recent decrease in this colony (609 years, [20–10,000] mean and 90 % HPD) (Fig. 5c).

Discussion

We generated three genetic data sets consisting of DNA sequences from mitochondrial and 14 nuclear regions and genotypes from 10 microsatellite loci to investigate genetic connectivity and demographic history of Providence petrel (*Pterodroma solandri*) colonies, an oceanic seabird IUCN uplisted as Vulnerable due to its restricted breeding range. High gene flow between the two remaining colonies of Providence petrel (Lord Howe Island and Phillip Island) was evident despite individuals at the two colonies showing different time of return to nesting sites. In addition, time of divergence among colonies appears recent, suggesting recent colonization of Phillip Island by individuals from Lord Howe Island. These results suggest high plasticity in behaviour rather than adaptive divergence in Providence petrels, and imply limited genetic risks surrounding the sustainability of the Phillip Island colony.

Contemporary genetic differentiation

The analyses conducted here on multiple datasets indicate high genetic connectivity between the two remaining populations of Providence petrel (Lord Howe Island and Phillip Island). While low genetic divergence among populations could also reflect high historical connectivity between populations that are now isolated (Palsboll et al. 2010), we also investigated contemporary gene flow among populations. We compared the variation of kinship coefficients within and between Providence petrel colonies (Lord Howe Island and Phillip Island), and showed that individuals coming from the same colony were as related genetically as individuals coming from different colonies; the best clustering of individuals was also independent of breeding locality. These results confirmed high current dispersal capacity of Providence petrels, which suggests that species-wide genetic diversity is being maintained by natural dispersal between colonies.

Time of colonization

Maximum likelihood estimates obtained from the isolation-with-migration model showed that Providence petrel

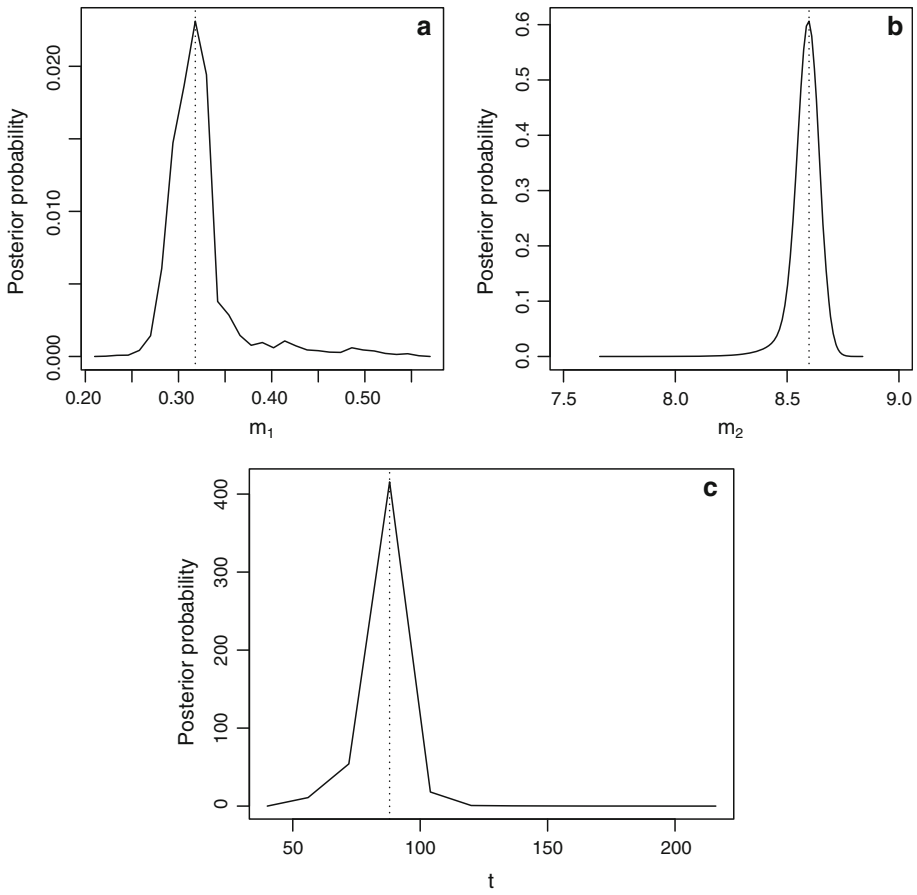

Fig. 4 Population divergence genetic parameters. Marginal posterior probability distributions for the Isolation with Migration demographic parameters. **a** migrants/generation from Lord Phillip Island to Lord Howe Island (m_1). **b** migrants/generation from Lord Howe Island to Phillip Island (m_2). **c** time of divergence (*t*, years)

colonies (Lord Howe Island and Phillip Island) became separated between 56 and 200 years ago. This suggests that individuals from Lord Howe Island were prospecting new habitats on Phillip Island after the extirpation of the Norfolk Island colony. These results indicate limited genetic risks surrounding the sustainability of the small Phillip Island colony of Providence petrels. Indeed, as dispersal of prospectors is positively related to the presence of conspecifics (Serrano et al. 2004), we can expect additional gene flow from Lord Howe Island to Phillip Island in the near future. Conversely, the fact that the Phillip Island colony was only discovered in 1986 may be explained by the first explorations of this small island in the 1970s (Priddel et al. 2010). We are presently analysing ancient DNA samples from the Norfolk Island colony to assess its historical connectivity with Lord Howe Island.

Behavioral difference in timing of colony attendance

Despite Providence petrel colonies being highly connected genetically, for the period of courtship and early incubation, Lord Howe Island individuals predominantly arrive at the colony during daylight, whereas Phillip Island individuals return to their breeding sites only after dusk. Numerous studies have illustrated the importance of behavioural plasticity as a fundamental trait of life history strategies in seabirds living in highly dynamic and variable environment (Falk et al. 2002; Paiva et al. 2009; Reed et al. 2009). Moreover, petrels have the capacity to use olfactory senses to find burrows at night, and this strategy is not exclusive to individuals showing nocturnal arrival at colonies (Bonadonna and Bretagnolle 2002; Dell'Ariccia and Bonadonna 2013). Individuals showing diurnal arrival are also able to use olfaction as the basic sensory input for homing at night, and use it if necessary (Dell'Ariccia and Bonadonna 2013). These observations imply that all petrels are able to return to their burrows at night, and that individuals alter their behaviour to environmental conditions without necessarily requiring genetic adaptation. Hence, it is likely that prospectors from Lord Howe Island have switched their behaviour on Phillip Island.

Earlier studies suggest that avoidance of predators is likely to be the main factor responsible for nocturnal colony arrival in small Procellariiformes (Keitt et al. 2004; McNeil et al. 1993; Warham 1990; Watanuki 1986). However, Providence petrels from Phillip Island as well as other seabird species possess a nocturnal arrival behaviour even in the absence of diurnal predators (Keitt et al. 2004).

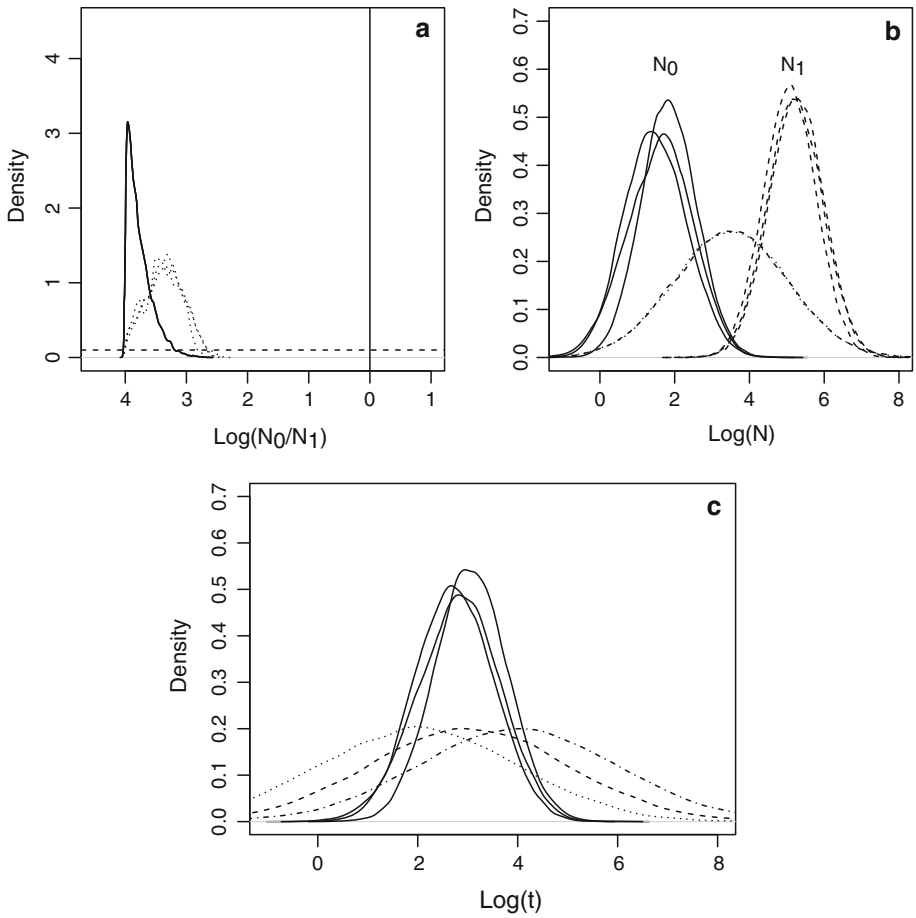

Fig. 5 Population size change in *P. solandri* using coalescent modeling of microsatellite data under MsVar v0.4 and Msvar v1.3. **a** posterior density distributions of the effective population size parameter $Log(N_0/N_1)$ from MsVar v0.4 where 0 indicates population stability, <0 decline, and >0 expansion. *Dotted curves* represent the linear model and *continuous curves* represent the exponential model. The *vertical solid line* represents the expected value of $Log(N_0/N_1)$ when the effective population size is stable. The straight *horizontal dotted line* represents the distribution of priors for comparison. **b** posterior density distributions of the current (N_0, *solid lines*) and the ancestral (N_1, *dotted lines*) effective population size parameter Log(N) using MsVar v1.3 under the exponential model. **c** posterior density distributions of the time parameter (Log(t), *solid lines*) since Providence petrels started to decline on Lord Howe Island using MsVar v1.3 under the exponential model. The inferior *dotted lines* in fig. **b** and **c** represent the prior distributions of each parameter for comparison

Considering establishment of Providence petrels on Phillip Island in the 1800 s, this behaviour may also be a recent adaptation to the presence of hawks on the island at the time of European settlement (Medway 2002b). Another explanation may be related to foraging, as has been observed for a number of seabird taxa (Baduini 2002; Dias et al. 2012). For example, Cory's shearwaters (*Calonectris diomedea*) show intraspecific variation in colony arrival depending on the marine region and abundance of prey, and are high flexibility in their daily routines (Dias et al. 2012). However, unpublished logger data from Lord Howe Island individuals suggests foraging throughout the Coral and Tasman Seas during the breeding season (Carlile, per. obs.), such that it is difficult to imagine differences in foraging locations between Lord Howe and Phillip Island individuals.

Demographic history

Coalescent modelling of microsatellites indicated a past bottleneck in Providence petrel. This significant decrease in population size is estimated to have occurred approximately 600 years ago. However, there is a broad uncertainty surrounding this date estimate. A survey of unconsolidated sediments on Lord Howe Island did not indicate human occupation of this island before the European era, beginning in 1788 (Anderson 2003). However, various pieces of evidence ascribed to origins in Tonga or New-Zealand (e.g., pieces of wrecked canoes, adzes made of local basalt and other wooden artefacts), as well as results of analyses of genetic variation in the Pacific rat (*Rattus exulans*) suggesting connectivity between Norfolk Island and New Zealand populations (Matisoo-Smith et al.

2001), constituted proof of Norfolk Island having been settled from New Zealand at about the thirteenth to fourteenth century (Anderson and White 2001; McCarthy 1934). Assuming that the Lord Howe colony was connected to the Norfolk Island colony (i.e., panmixia), the commencement of the bottleneck may be explained by the introduction Pacific rats or kiore (*Rattus exulans*) on Norfolk Island 600 year B.P., as kiore is well known for having affected seabird species on other islands (Holdaway 1999; Rayner et al. 2007; Tennyson and Martinson 2006; Towns 2009). Polynesians may have also directly exploited the Norfolk population, as it has been seen elsewhere (Boessenkool et al. 2009; Holdaway and Jacomb 2000; Worthy 1999). Additionally or alternatively, given the arrival of Polynesians in New Zealand 700 year B.P. (Wilmshurst and Higham 2004), they may have also encountered Lord Howe Island at the same period. They may not have settled, which could explain lack of archaeological evidence, but allowed kiore (*Rattus exulans*) to colonise. Kiore may then have disappeared after the introduction of the ship rat (*Rattus rattus*) in 1918 (Hindwood 1940). However, there is no evidence for Kiore ever having occupied Lord Howe Island.

Conservation implications

The local extirpation of Providence petrels has had a severe impact on the terrestrial ecosystem of Norfolk Island, particularly through the deficiency of phosphorus leading to Norfolk Island pines (*Araucaria heterophylla*) being highly affected by the root-rotting fungus *Phellinus noxius* (Holdaway and Christian 2010). To reduce the extinction risk of Providence petrels and to provide key nutrients for the regeneration of threatened native forests and associated species, a plan to re-establish a colony of Providence petrels on Norfolk Island using Lord Howe Island individuals has been proposed. Here we show that the small colony of Providence petrels breeding on Phillip Island is genetically connected to the Lord Howe Island colony. These results indicate limited risks surrounding the proposed translocation of Lord Howe Island individuals to re-establish a colony on Norfolk Island with respect to potential genetic novelty of the Phillip Island colony. In addition, as colonisation of Phillip Island has been recent, further gene flow will likely occur from Lord Howe Island to the Norfolk Island group, including the new translocated colony, reducing risks of inbreeding depression following translocation. While kiore is still present on Norfolk Island, this was not the proximate cause for Providence petrel extinction from Norfolk Island. There is no obvious threat to other avian species on the island through this reintroduction.

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