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Comprehensive evidence for subspecies designations in Cook's Petrel *Pterodroma cookii* with implications for conservation management

MATT J. RAYNER[1*], AYLA L. VAN LOENEN[2*], LARA D. SHEPHERD[3], ILINA CUBRINOVSKA[2], R. PAUL SCOFIELD[4], ALAN J. D. TENNYSON[3], MICHAEL BUNCE[5] and TAMMY E. STEEVES[2]

[1]*Auckland Museum, Private Bag 92018, Auckland, 1141, New Zealand.*
[2]*School of Biological Sciences, University of Canterbury, Christchurch, New Zealand.*
[3]*Museum of New Zealand Te Papa Tongarewa, PO Box 467, Wellington, New Zealand.*
[4]*Canterbury Museum, Christchurch, New Zealand.*
[5]*Trace and Environmental DNA (TrEnD) Laboratory, School of Molecular and Life Sciences, Curtin University, Perth, Western Australia 6102, Australia.*

**Authors for correspondence (both authors contributed equally);*
emails: mrayner@aucklandmuseum.com; ayla.vanloenen@gmail.com

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Summary

Cook's Petrel *Pterodroma cookii* is an endemic New Zealand seabird that has experienced a large range decline since the arrival of humans and now only breeds on two offshore islands (Te Hauturu-o-Toi/Little Barrier Island and Whenua Hou/Codfish Island) at the extreme ends of its former distribution. Morphological, behavioural, and mitochondrial *cytochrome oxidase 1* (CO1) sequence data led a previous study to recognise the two extant populations as distinct conservation management units. Here, we further examine the genetic relationship between the extant populations using two nuclear introns (*β-fibint7* and *PAX*). Using one mitochondrial locus (CO1), we also investigate the past distribution of a single nucleotide polymorphism (SNP) that differentiates the modern populations using bone and museum skins sourced from within its former range across New Zealand's North and South Islands. We found significant population genetic structure between the two extant Cook's Petrel populations for one of the two nuclear introns (*β-fibint7*). The mitochondrial DNA CO1 analysis indicated that the SNP variant found in the Codfish Island population was formerly widely distributed across both the North and South Islands, whereas the Little Barrier Island variant was detected only in North Island samples. We argue that these combined data support the recognition of the extant populations as different subspecies. Previous names for these taxa exist, thus Cook's Petrel from Little Barrier Island becomes *Pterodroma cookii cookii* and Cook's Petrel from Codfish Island becomes *P. c. orientalis*. Furthermore, we suggest that both genetic and non-genetic data should be taken into consideration when planning future mainland translocations. Namely, any translocations on the South Island should be sourced from Codfish Island and future translocations on the North Island should continue to be sourced from Little Barrier Island only.

Keywords: Cook's Petrel, conservation genetics, translocation, seabird conservation.

Introduction

Analysis of genetic data in modern populations has proven to be a powerful tool for reconstructing crucial aspects of the evolutionary history of threatened species, thus informing conservation management (Willerslev and Cooper 2005, Rohland and Hofreiter 2007, Leonard 2008, Gangloff *et al*. 2012a). Similarly, the analysis of ancient DNA (aDNA) is valued as a means to compare past and present levels of genetic variation (Shepherd and Lambert 2008, Shepherd *et al*. 2012), identify the ranges of morphologically indistinct taxa (Russello *et al*. 2010, Steeves *et al*. 2010, Robertson *et al*. 2011, Spurgin *et al*. 2014) and provide accurate species delineation (Boessenkool *et al*. 2009). Such data are valuable for conservation managers seeking diagnostic tools to accurately assign conservation status and provide guidance for the restoration of species that have undergone extreme range declines (Hofkin *et al*. 2003, Valentine *et al*. 2007, Russello *et al*. 2010).

The New Zealand archipelago is a globally significant example of avian biodiversity loss with at least 60 species of endemic birds becoming extinct since human colonisation 750 years ago and many other taxa such as seabirds, experiencing extreme range retractions (Worthy and Holdaway 2002). Cook's Petrel *Pterodroma cookii* is a small endemic seabird that has undergone massive population reductions since human colonisation of New Zealand (Imber *et al*. 2003, Wilmshurst *et al*. 2011). Today Cook's Petrels breed only at the northern and southern extremes of their former range on Te Hauturu-o-Toi/Little Barrier Island (LBI, ~286,000 breeding pairs; Rayner *et al*. 2007) and Whenua Hou/Codfish Island (CDF, ~5,000 breeding pairs; Rayner *et al*. 2008a), separated by approximately 1,300 km (Figure 1). Both populations are recovering following introduced predator eradication, the CDF island population notably had declined to less than 100 breeding pairs by predation from introduced Weka *Gallirallus australis* and Pacific rat *Rattus exulans* (Bartle *et al*. 1990, Imber *et al*. 2003). Historically Cook's Petrels bred throughout New Zealand in vast colonies, as evidenced by extensive Holocene deposits found in cave and dune systems and also supported by records from early European explorers and Māori oral history (Imber *et al*. 2003).

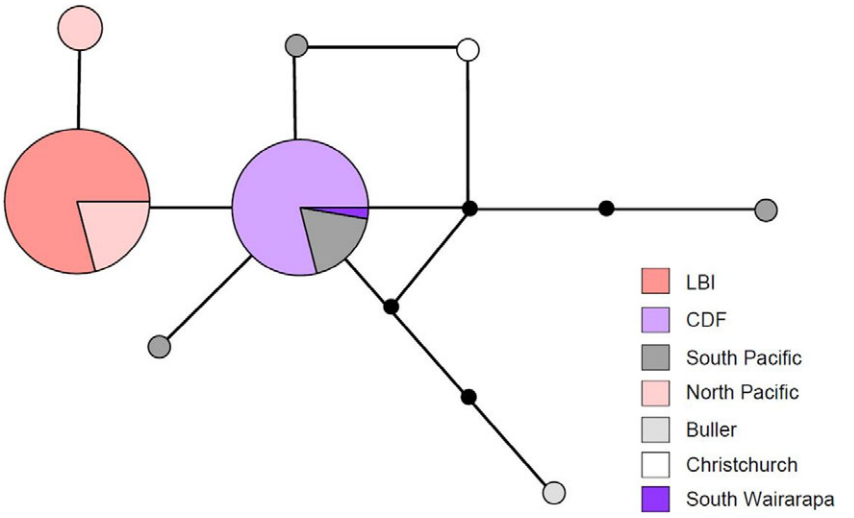

Figure 1. Median-joining network for 375 bp of mitochondrial COI sequence from modern, historic and ancient samples of Cook's Petrel (n = 90). Haplotypes are colour-coded by collection location. The size of each circle is proportional to haplotype frequency. Connecting lines represent a single mutation and solid black circles correspond to missing haplotypes. Buller, Christchurch and South Wairarapa haplotypes were found in historic samples TP08, TES05 and TES02, respectively (see Table S5 for details).

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Given the historic ubiquity of Cook's Petrel and increasing recognition of seabirds as nutrient donors in New Zealand terrestrial ecosystems (Worthy and Holdaway 2002, Towns 2018), conservation management efforts have recently focused on re-establishing lost populations on mainland New Zealand through a chick translocation program (Miskelly *et al*. 2009). However, such actions are limited by a lack of understanding of the evolutionary history and extirpation dynamics of this once widely distributed New Zealand endemic, specifically a lack of information regarding the genetic make-up of extirpated populations across both North and South Islands.

Morphological, behavioural, and genetic studies have identified the two remaining populations of Cook's Petrels as distinct conservation management units. As reviewed in Rayner *et al*. (2010a), Imber (2003) identified differences in body mass between smaller birds on LBI and larger birds on CDF, which parallels significant differences in the breeding season foraging habitat use (Rayner *et al*. 2008b, 2010b). Moreover, the asynchronous breeding and migration schedules of the two populations (approximately six weeks apart), as well as separate nonbreeding distributions, are a recognised barrier to gene flow through local adaptation in combination with strong natal philopatry (Rayner *et al*. 2011). In the first genetic study of the species, Rayner *et al*. (2010a) identified significant population genetic structure between the extant populations in mitochondrial DNA (mtDNA) *cytochrome oxidase 1* (COI) sequences. Five mtDNA haplotypes were detected, four in the LBI population and one in the CDF population. No mtDNA haplotypes were shared between populations and there was a single fixed polymorphism that could be used to separate samples from both contemporary and historic (museum skin) individuals collected in the eastern Pacific Ocean (Rayner *et al*. 2010a, 2011). As a result of these studies, it was recommended that the LBI and CDF populations be treated as distinct conservation management units. However, taxonomic designation and an understanding of the level of genetic diversity within each population require further analysis integrating nuclear markers and data from extirpated populations (Rayner *et al*. 2010a).

To establish new populations of Cook's Petrel, more than 500 chicks from the large LBI population have been translocated to predator-free sites in the North Island of New Zealand since 2010. In the absence of information on the historical distribution of Cook's Petrel genotypes on the New Zealand mainland, the decision to source birds from the northern LBI population was based on geographic proximity alone. Given the availability of Cook's Petrel fossils and museum skins from throughout the main islands of New Zealand, analysis of aDNA presents an opportunity to understand patterns of genetic diversity in extirpated populations of this taxon.

Lack of time-stamped data in fragmented populations can result in a misleading picture of former connectivity and species boundaries (Haouchar *et al*. 2016). Accordingly, this study set out to: (i) investigate what, if any, genetic structure was present in Cook's Petrel populations across its former range, and (ii) further clarify the relationship between the extant populations and thus the taxonomic status of the LBI and CDF populations using both mitochondrial and nuclear loci. By resolving these issues our final aim was to: (iii) integrate ancient and modern DNA to inform conservation management of the species through population restoration.

Methods

DNA extractions, PCR amplification and sequencing

To augment the existing mitochondrial CO1 sequence data for modern and historic Cook's Petrels collected from CDF ($n = 19$), LBI ($n = 26$), North Pacific ($n = 9$) and South Pacific ($n = 10$) (Rayner *et al*. 2010a, 2011), DNA was extracted from 23 additional blood samples collected by M. Rayner (LBI, $n = 12$, CDF, $n = 11$) (Table S1 in the Online Supplementary Material) with an Invitrogen PureLink™ Genomic DNA kit according to the manufacturer's protocol for mammalian tissue with the following modifications: the initial incubation step was increased to 18–19 hours, and the proteinase-K was added after the initial incubation step.

Ancient specimens from throughout the former range of Cook's Petrel (Figure 1, Table S2) were processed in dedicated ancient DNA facilities (University of Canterbury, Murdoch University and

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Museum of New Zealand Te Papa Tongarewa) following established standards for ancient DNA work (Shapiro and Hofreiter 2012). For samples processed at the latter, DNA was extracted using the phenol-chloroform protocol detailed in Shepherd and Lambert (2008). DNA extractions at the other two facilities used previously published column-based extraction protocols for bone (Allentoft *et al*. 2012) and toepad (White *et al*. 2012). Potential contamination was monitored through extraction and PCR negative controls. A subset of samples extracted at Murdoch were also extracted, amplified, and sequenced at UC for authentication (independent replication), and a subset of samples extracted at Te Papa were also amplified and sequenced at UC for authentication (reproducibility). Sequences were only included in the analyses if they were recovered in a minimum of two independent reactions per sample.

A 692 bp fragment of the mitochondrial CO1 gene was amplified in modern samples using CO1-F1B/CO1-R1B PCR Assay (Gangloff *et al*. 2012a). Two overlapping fragments were amplified in historic and ancient samples to give a total of 375 bp of CO1 sequence using AWCF1/AWCintR2 and LCRintF2/AWCintR3 PCR assays (for details see Patel *et al*. 2010, Rayner *et al*. 2011). For degraded samples that could not be amplified with the above primers, we designed additional overlapping primer pairs with M13 tags (underlined) to amplify an even smaller section (16 bp) of the CO1 region (aDNA_CO1mini_2F CO1 CACGACGTTGTAAAACGACTTGGAAACTGACTAGTCCCC/aDNA_CO1mini_2R CO1 GGATAACAATTTCACACAGGACGTGGGAATGCTATGTCAG and aDNA_CO1mini_3F CO1 CACGACGTTGTAAAACGACGAAACTGACTAGTCCCCCTT/aDNA_CO1mini_3R CO1 GGATAACAATTTCACACAGGGTGGGAATGCTATGTCAGGG). This region specifically included the 'diagnostic' SNP reported in Rayner *et al*. (2010a, 2011), between modern individuals from LBI and CDF islands (see Results).

Partial fragments of two nuclear introns were also amplified from the modern samples: a 478 bp region of the *PAX interacting protein 1* (*PAX*) locus using PAX_20F/PAX_21R (Leonard 2008) and a 531 bp fragment of the *β-fibrinogen intron 7* (*β-fibint7*) locus using modified primers from Prychitko and Moore (2003): FIB-B17Umodified β-fibint7 TGGATGGTACGTACTTGCATT/FIB-B17internalR β-fibint7 TCCCCAATCTAAACAATTCCTC.

All PCRs for modern samples (25μL) included 1x PCR buffer (Bioline^{TM}), 2mM $MgCl_2$, 0.4μM of each primer, 2.5mM dNTPs, 1U of BIOTAQ^{TM} DNA polymerase, and ~10ng of DNA. For all modern samples, PCR thermocycling conditions were: 95°C for 90 sec, followed by 30 cycles of 95°C for 30 sec, 53–60.7°C for 30 sec (53°C for CO1, 59°C for *β-fibint7*, 60.7°C for *PAX*), 72°C for 45 sec, and a final extension at 72°C for 3 min. All PCRs for ancient samples (25μL) included 1x Amplitaq Gold 360 Master Mix, 0.4μM forward and reverse primers, and 2-4μL of DNA. For all ancient samples, PCR thermocycling conditions were: 95°C for 10 min, followed by 10 cycles of 95°C for 30 sec, 55°C for 30 sec, 72°C for 30 sec, followed by a further 30 cycles of 95°C for 30 sec, 50°C for 30 sec, 72°C for 30 sec, and a final extension at 72°C for 3 min. PCR products were purified for sequencing using AcroPrep^{TM} Advance Filter Plates (PALL). Sequencing was performed in both forward and reverse directions using Big Dye 3.1 chemistry on an Applied Biosystems 3130x1 Genetic Analyser. All sequences were aligned using Geneious 6.1.4 (Biomatters) and all variable sites were confirmed by eye.

Sequence analyses

To address our first aim, we calculated genetic differentiation (Φ_{ST}) and standard molecular diversity indices for the mitochondrial CO1 locus for the extant populations of Cook's Petrel using Arlequin 3.5.1.2 (Excoffier and Lischer 2010). We also constructed median-joining networks (Bandelt *et al*. 1999) for modern, historic and ancient mitochondrial CO1 haplotypes using Network 4.613 (www.fluxus-engineering.com) with either transitions (ti) and transversions (tv) equally weighted or using the ti:tv ratio calculated by the AIC in jModeltest 2.1.7 (Darriba *et al*. 2012). We plotted the distribution of the 'diagnostic' SNP (nucleotide position 156) across the former range of Cook's Petrel.

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To address our second aim, DnaSP 5.10.1 (Librado and Rozas 2009) was used to reconstruct haplotype phases for β-fibint7 and PAX according to the algorithms provided by PHASE 2.1 (Stephens *et al*. 2001, Stephens and Donnelly 2003). The haplotypes were reconstructed using the following parameters: no recombination, 1,000 MCMC iterations, with 1,000 iterations of burn-in, and an output probability threshold of 0.6 (Garrick *et al*. 2010). Analyses were repeated three times using different starting seed values and consistency across runs checked by eye. Recombination within β-fibint7 and PAX was tested using TOPALI 2.5 (Milne *et al*. 2008). Genetic differentiation (ϕST) and standard molecular diversity indices were calculated for each locus as per the above. Median-joining networks were constructed for each locus as per the above.

Results

We obtained CO1 sequences for all 23 additional modern samples. Of the 28 historic and ancient samples, only three amplified for the 375 bp fragment of CO1 (Table S2). However, a further 20 samples were successfully sequenced for at least the 16 bp CO1 fragment containing the 'diagnostic' SNP at nucleotide position 156 (Table S2).

Among all available modern, historic, and ancient Cook's Petrel samples (n = 90), there were nine variable sites found within the 375 bp region of the CO1 locus, of which seven were transitions and three were transversions, that defined eight haplotypes (Table S1). There was significant genetic population structure between the extant Cook's Petrel populations on LBI and CDF (φ_{ST} = 1.00, P <0.0001). The relationships among mitochondrial CO1 haplotypes are shown in Figure 1. The same network was produced with an equal ti:tv ratio and a ti:tv ratio of 2.83, as calculated in jModeltest. Two of the ancient specimens had novel haplotypes that differed from their most closely related haplotype by one (TES05) or three (TP08) substitutions. The third ancient sample shared a haplotype common in the modern CDF population.

The distribution of the 'diagnostic' CO1 SNP at site 156 is mapped in Figure 2. The SNP defining the CDF population (C) was found in ancient samples from throughout the South Island and also in samples from the North Island south of Mahoenui, the SNP defining the LBI population (T) was identified in five ancient populations and co-occurred with the CDF SNP in two North Island locations (Featherston and Mahoenui).

Nuclear PAX interacting protein 1 (PAX) and β-fibrinogen intron 7 (β-fibint7)

For the two extant populations of Cook's Petrel, there were 19 variable sites, 10 of which were transitions and nine of which were transversions. The phased haplotypes were consistent across runs and defined 20 haplotypes (Table S2). The networks of relationships between the PAX haplotypes resulting from the different PHASE runs were identical, as were the networks using an equal ti:tv ratio or a ti:tv ratio of 0.78, as calculated in jModeltest (Figure 3). Haplotype diversity (h) was 0.92 and nucleotide diversity (π) was = 0.0068. Twelve haplotypes were found at LBI, seven of which were unique (h = 0.90, π = 0.0058) and 13 haplotypes were found at CDF, eight of which were unique (h = 0.95, π = 0.0076). There was no significant genetic structure for the PAX locus between the two extant populations (ϕST <0.001, P = 0.44).

For the β-fibint7 locus, there were 12 variable sites, nine of which were transitions and three were transversions. The phased haplotypes were consistent across runs and defined 15 haplotypes (Table S3) (h = 0.86, π = 0.0056). Identical networks of haplotype relationships were reconstructed from all three PHASE runs and using an equal ti:tv ratio or a ti:tv ratio of 3.17, as calculated in jModeltest (Figure 3). Twelve haplotypes were found at LBI, eight of which were unique (h = 0.79, π = 0.0046). Seven haplotypes were found at CDF, three of which were unique (h = 0.81, π = 0.0058). There was moderate genetic structure for the β-fibint7 locus between the two extant Cook's Petrel populations (ϕ_{ST} = 0.12, P = 0.0029).

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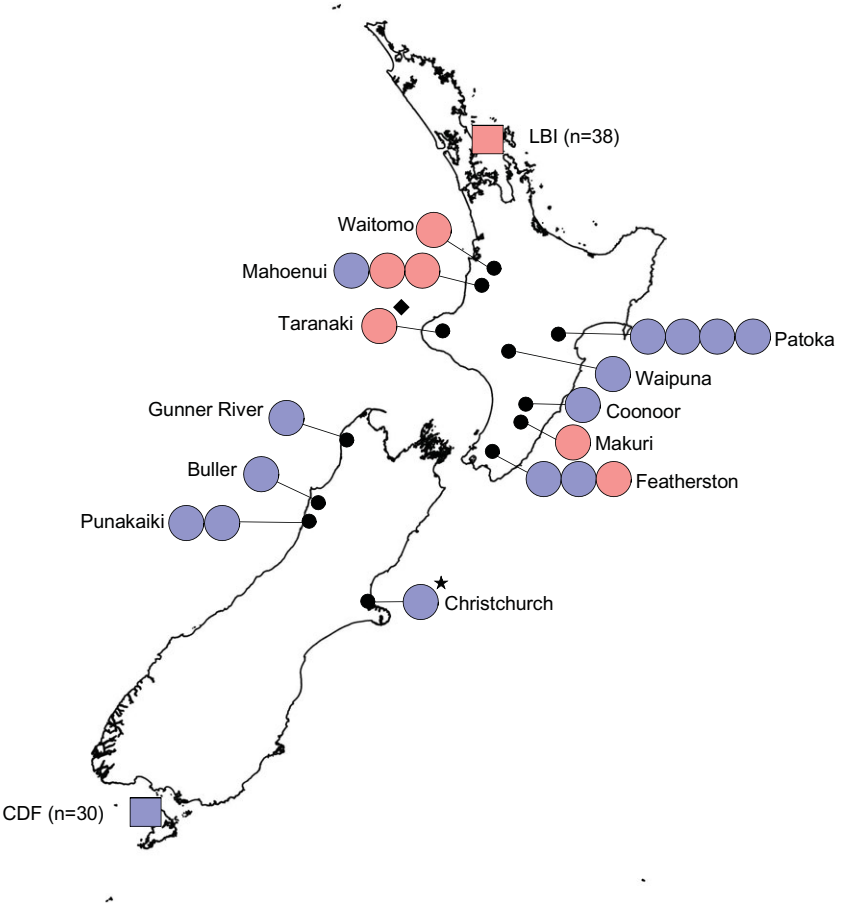

Figure 2. Distribution of the 'diagnostic' Cook's Petrel mitochondrial CO1 SNP (Rayner *et al.* 2010a, 2011). Extant populations represented by squares and extirpated populations by circles. Pink and purple denote a T and a C at site 156, respectively (see text for details). The diamond indicates the holotype specimen of *P. cookii* (Gray, 1843) and the star indicates a specimen from an unknown provenance that was collected after crashing into a streetlight.

Discussion

Phylogeography of Cook's Petrel across its historic range.

Our phylogeographic analysis of Cook's Petrel across New Zealand supports existing research showing that genetic structuring can occur in populations at the ends of a broad geographic range (Stephens *et al.* 2001). There is little evidence for a distinct phylogeographic break in historic mainland populations as observed in studies of other New Zealand avifauna (Shepherd *et al.* 2012, Rawlence *et al.* 2016, 2017). Instead, our results demonstrate a zone of co-occurring mitochondrial lineages, particularly in the North Island, more reflective of a haplotype cline.

Pterodroma petrels are among the most mobile birds on earth, routinely travelling a thousand or more kilometres in a single day during oceanic foraging trips (Boessenkool *et al.* 2009, Rayner *et al.* 2011, 2012). Thus, it is unsurprising that historic populations breeding on the North Island of New Zealand do not show the same level of phylogeographic structuring as other New Zealand

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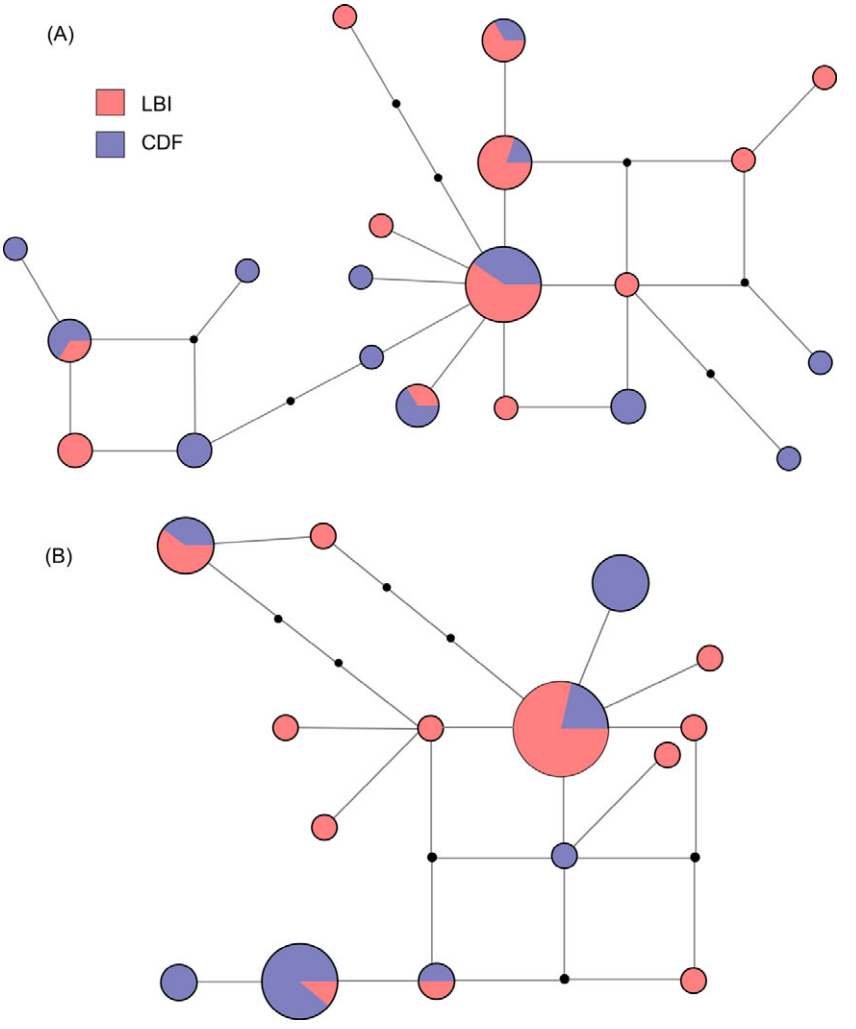

Figure 3. Median-joining networks for modern samples of Cook's Petrel (A) PAX phased haplotypes and (B) *β-fibint7* phased haplotypes. Haplotypes are colour-coded by location. The size of each circle is proportional to haplotype frequency. Connecting lines represent a single mutation and solid black circles correspond to missing haplotypes.

seabirds, such as some shag species, which by comparison are sedentary and remain in close proximity year round to breeding colonies (Rawlence *et al.* 2016). We acknowledge that the lack of a distinct phylogeographic break in Cook's Petrel, compared with other New Zealand seabirds, could be attributed to sampling of ancient bones not related to local breeding colonies. However, we consider this unlikely given the strong natal philopatry of *Pterodroma* petrels in general (Brooke 2004), which has been shown to impact genetic structure between populations breeding on differing islands at close geographic proximity (Welch *et al.* 2012a).

Our results are consistent with previous ancient DNA studies demonstrating character fixation in extant populations supported by human-mediated extinctions across a species' historic range (Stephens and Donnelly 2003, Rohland and Hofreiter 2007). In the case of Cook's Petrel our study suggests that human-mediated extinction of intermediary populations across a latitudinal cline has

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reinforced the differentiation of northern and southern Cook's Petrel lineages. This is demonstrated by character fixation in the mitochondrial CO1 locus, and additional differentiation in the nuclear *β-fibint7* locus. However, in the case of Cook's Petrel, anthropogenic character fixation has supported an existing evolutionary process already under way, resulting in the differentiation at the northern and southern ends of the species range (Stephens *et al.* 2001). Ecological isolating mechanisms including breeding and migration timing (allochrony), foraging habitat selection and natal philopatry provide a robust framework for explaining the divergence of seabird populations in both allopatry and sympatry (Friesen *et al.* 2007a, 2007b, Boessenkool *et al.* 2009, Rayner *et al.* 2011, Wilmshurst *et al.* 2011, Friesen 2015). However, how these mechanisms contributed to a prehistoric phenotypic and genotypic cline across intermediate (locally) extinct populations of Cook's Petrel requires further study.

In the meantime, when only a single locus, such as mtDNA, is used for phylogeographic reconstruction then the effects of selection, sex-biased dispersal or the stochastic nature of the coalescence process could result in a biased view of species history. Studies have shown that mtDNA is a useful marker, compared with nuclear markers, for detecting recent population differentiation in avian taxa because of its rapid coalescent time (Zink and Barrowclough 2008, Hung *et al.* 2016). However, including additional independently evolving nuclear markers improves the power of molecular data to test phylogeographic hypotheses (Toews and Brelsford 2012).

Taxonomic status of extant Cook's Petrel populations

Typical of nuclear intron loci, extant Cook's Petrels exhibit less phylogeographic structure for PAX and *β-fibint7* than for the mitochondrial CO1 locus (Zink and Barrowclough 2008, Edwards and Bensch 2009). Similarly, it is typical for some nuclear introns, particularly *β-fibint7* in birds, to exhibit more phylogeographic structure than others due to stochastic lineage sorting (Gangloff *et al.* 2012b, Morris-Pocock et al. 2016). Detecting relatively weak or no phylogeographic structure using nuclear markers may indicate male-mediated gene flow (e.g. Burg and Croxall 2001, but see Karl *et al.* 2012), but there is limited evidence of male-biased dispersal in seabirds, particularly for *Pterodroma* petrels (Gangloff *et al.* 2012b, Iglesias-Vasquez *et al.* 2017). Further, the differences observed in this study are consistent with the four-fold difference in effective population size between mitochondrial and nuclear markers (Zink and Barrowclough 2008, Edwards and Bensch 2009). Thus, the *β-fibint7* and CO1 networks, combined with respective estimates of moderate to strong population genetic structure, are congruent with Rayner *et al.* (2010a, 2011) and indicate that the two extant populations of Cook's Petrel are genetically isolated and thus warrant taxonomic revision.

Taxonomic justification

The current analysis complements the morphological, behavioural, and ecological traits outlined in the introduction that separate the extant Cook's Petrel populations (Imber *et al.* 2003, Rayner *et al.* 2008a, 2011). The extent of these differences is comparable or greater than levels of differentiation between seabird lineages considered to be distinct subspecies (Bandelt *et al.* 1999, Brooke and Rowe 1996, Allentoft *et al.* 2012, Welch *et al.* 2012b, Iglesias-Vasquez *et al.* 2017). For example in comparison with our study, Iglesias-Vasquez *et al.* (2017) found less genetic differentiation between the two subspecies of Australian and New Caledonian Gould's Petrel *Pterodroma leucoptera* for the CO1 locus and similar levels of differentiation for nuclear loci. These results suggest the two extant Cook's Petrel populations are sufficiently divergent to warrant recognition as distinct subspecies.

Accordingly, we recognise CDF breeding Cook's Petrels as belonging to the taxon *P. cookii orientalis* (Murphy, 1929). Murphy (1929) described this taxon based on body size and plumage characteristics of birds collected off the coast of Peru, which is now known to be within the core of the CDF Cook's Petrel non-breeding habitat (Rayner *et al.* 2011). Moreover, Rayner *et al.* (2011)

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generated CO1 sequences from several of these specimens held in the American Museum of Natural History (AMNH), including a paratype (AMNH 446060). All specimens, including AMNH 446060, were collected at the same time and place as the holotype, all were identified by the same expert (Rollo Beck), and share the same 'diagnostic' SNP identified as southern Cook's Petrel in Rayner *et al.* (2010a). Based on these combined data, AMNH declined our request to destructively sample the holotype. We advocate that LBI breeding Cook's Petrel should be recognised as *P. cookii cookii* (G. R. Gray, 1843), as per the results of Matthews (1912). This taxon was originally described by George Gray from the holotype (which has a haplotype typical of the northern birds) that has recently been shown (Medway 2004) to have been collected at the Mangaoraka Stream near Kaimiro, north Taranaki, New Zealand (see Figure 1).

Taxonomic recommendation

ORDER: Procellariiformes Fürbringer, 1888
FAMILY Procellaridae Leach, 1820
GENUS *Pterodroma* Bonaparte, 1856

Pterodroma cookii cookii *Gray, 1843*

Procellaria cooki Gray, 1843 in Dieffenbach, Travels in New Zealand 2:199. Type locality: Mangaoraka Stream near Kaimiro, North Taranaki (*fide* Medway 2004).

Formerly bred throughout the mountains of the northern North Island of New Zealand. Breeding now restricted naturally to Little Barrier Island with mainly unsuccessful breeding attempts on Great Barrier Island in the presence of introduced mammalian predators. Outcome of two translocations of chicks to the eastern north Island (Hawkes Bay) is awaiting confirmation. Shown to spend the non-breeding season in the north-eastern South Pacific Ocean with arrival on breeding grounds in late September and egg-laying in November (Rayner *et al.* 2011).

Pterodroma cookii orientalis *Murphy, 1929*

Pterodroma cookii orientalis Murphy, 1929: *American Museum Novitiates* 370: 5 Type locality: 200 miles west of Callao, Peru.

Formerly bred throughout the mountains of the southern North Island and the South Island of New Zealand and Stewart Island and its surrounding islets. Breeding now restricted naturally to Codfish Island. Shown to spend the non-breeding season in the central-eastern South Pacific Ocean arriving on breeding grounds in November and laying in December (Rayner *et al.* 2011).

Conservation implications

Despite apparent past geographic overlap on the North Island (not taking age of fossil sites into consideration), available genetic and non-genetic data support the subspecies status of the extant populations of Cook's Petrel which has implications for conservation management. There are currently management efforts attempting, or planning to attempt, the restoration of Cook's Petrel populations on the New Zealand mainland to gain ecological benefits of seabird based nutrient subsidies. To date, these efforts, which include chick translocations and acoustic attraction, have been focused on the larger LBI population as a source population for geographically proximate translocation sites as recommended by Rayner *et al.* (2010a). However, we argue that all available data, genetic and non-genetic, should be taken into consideration when planning future mainland translocations. We acknowledge that some might suggest that individuals should be sourced from both CDF and LBI for future translocation to the North Island given that the genetic data in this study show historic co-occurrence of northern and southern Cook's Petrel mitochondrial lineages on the North Island. However, we argue that sourcing individuals from two populations that

exhibit substantially different migratory behaviour and asynchronous breeding times/seasons would introduce a risk of translocation failure and future translocations to the North Island should continue to be sourced from Cook's Petrel from LBI only. Accordingly, these data advocate any future translocation to the South Island be sourced from Cook's petrel from CDF only to maximise recovery of this relict population.

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Supplementary Materials

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0959270920000350.

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