Distribution and gene-flow in a hybridising population of *Pterodroma* petrels

Katherine Alice Booth Jones

A dissertation submitted for the degree of

Doctor of Philosophy

University College London

ZSL
INSTITUTE
OF ZOOLOGY

UCL

Wing-runners, Katherine Booth Jones, 2016. A dark morph and a pale morph petrel perform their chasing display above the camp region of Round Island, over an iconic backdrop of Latania palms.

Declaration

I, Katherine Alice Booth Jones confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis, and below:

Chapter 2:

Co-authors: Malcolm A.C. Nicoll, Claire Raisin, Deborah A. Dawson, Helen Hipperson, Gavin J. Horsburgh, Stefanie M.H. Ismar, Paul Sweet, Carl G. Jones, Vikash Tatayah, and Ken Norris.

KABJ deployed geolocators, collected blood and museum samples, performed lab work and analysis and wrote the manuscript and Appendix A (excluding library development). MACN devised the experiment, deployed and recovered geolocators, collected blood and museum samples and provided comments on the manuscript. CR developed the library of markers and wrote the library development section of Appendix A. DAD provided guidance on lab work and analysis and provided comments on the manuscript. HH provided guidance on analysis and comments on the manuscript. GJH supported lab work and analysis. SMHI provided blood samples from Kermadec petrels of the Kermadec Islands. PS facilitated access to the Whitney South Seas Expedition petrel skin collection at the American Museum of Natural History. CJ and VT facilitated access to Round Island and data on Round Island petrels through the Mauritian Wildlife Foundation. KN devised the experiment, deployed and recovered geolocators, collected blood and museum samples and provided comments on the manuscript.

Chapter 3:

Co-authors: Robin Freeman, Malcolm A.C. Nicoll, Michelle Antolos, Andrés Lopez-Sepulcre, Norman Ratcliffe, Carl Jones, Vikash Tatayah, and Ken Norris**.**

KABJ deployed geolocators, modified the R scripts, performed analysis and wrote the manuscript. The original MATLAB script for removing shading events from geolocator light files was obtained with permission from MA, and initially translated into R programming code by ALS. MA and ALS both provided comments on the manuscript. Further modifications of the R scripts for the CleanLight process were made by RF, and

the Shiny app was developed by RF, who also provided advice on the testing of the scripts and comments on the manuscript. MACN and KN deployed and recovered geolocators and provided comments on the manuscript. NR provided advice on the use of BAS geolocators and comments on the manuscript. CJ and VT facilitated access to Round Island and data on Round Island petrels through the Mauritian Wildlife Foundation.

Chapter 4:

Co-authors: Malcolm A.C. Nicoll, Garth Holloway, Carl G. Jones, Vikash Tatayah, and Ken Norris.

KABJ deployed geolocators, performed analysis and wrote the manuscript and Appendix C. MACN and KN devised the experiment, deployed and recovered geolocators, and provided comments on the manuscript. GH developed and executed the Bayesian Mixtures Analysis in MATLAB. CJ and VT facilitated access to Round Island and data on Round Island petrels through the Mauritian Wildlife Foundation.

Chapter 5:

Co-authors: Malcolm A.C. Nicoll, Carl G. Jones, Vikash Tatayah, and Ken Norris.

KABJ deployed geolocators, performed analysis and wrote the manuscript and Appendix D. MACN and KN devised the experiment, deployed and recovered geolocators, and provided comments on the manuscript. CJ and VT facilitated access to Round Island and data on Round Island petrels through the Mauritian Wildlife Foundation.

10th August 2016

Abstract

Albatrosses and petrels (Order Procellariiformes) are renowned for the huge distances they can cover at sea, and since the advent of tracking technology their pelagic lifestyles are generally well studied. However, tropical species are under-represented in the literature, and may be particularly flexible in their behaviour since tropical oceans are oligotrophic and prey availability is often patchily distributed.

Round Island petrels breed in such an environment off the coast of Mauritius in the south-western Indian Ocean. Whilst originally identified as Trindade petrels (*Pteromdroma arminjoniana*), it has recently been revealed that this population is in fact a mixed, hybridizing population with at least two additional species, namely the Kermadec and Herald petrels (*P. neglecta and P. heraldica*). However, to date no research has been conducted on the colony-based at-sea distribution of these petrels, or how their mixed ancestry may influence their distribution at sea.

In this thesis I firstly explore the possibility that Round Island may not be the only point of contact between these species and find that migration and introgression between wide-ranging *Pterodroma* may be more common than previously thought.

I go on to develop a novel data cleaning method to enable the analysis of geolocation data from Round Island petrels, and use that data to describe for the first time their at-sea distribution and the extensive within-population variation in these patterns.

Finally, I use a combination of tracking and microsatellite genotype data to ultimately weigh the influence of individual genetic background and the wider seasonal environment on distribution variability around the breeding colony.

The Round Island petrel population is a stronghold where seabird populations globally are in decline. This thesis adds to the limited literature on ecology of tropical petrel species, and highlights the importance of considering behavioural and genetic diversity in future conservation plans.

Acknowledgements

Firstly, I'd like to thank my supervisors Ken Norris, Malcolm Nicoll, Vikash Tatayah and Kate Jones. Vikash has been an incredible help in organising everything to do with Round Island, and his thesis on the petrels has been a constant font of information for me throughout my PhD. Kate agreed to take me on after Ken, Malc and I moved from the University of Reading to the Institute of Zoology for the final two years of my PhD, and as such was exposed to a few slightly hysterical meetings. Thanks for being understanding and for bringing some structure to our supervisory meetings! Ken and Malc have been fantastic supervisors, providing me with inspiration, solid support and more than a few laughs, from tropical desert islands to dingy downtown New York bars. I can't thank you enough for taking me on after my degree and giving me the opportunity to tackle this dream PhD, I have loved every minute.

I'd like to thank the Mauritian Wildlife Foundation staff and volunteers and the Mauritian Government National Parks and Conservation Service for their assistance in providing ringing data, fitting geolocators and blood sampling.

Many thanks to Robin Freeman for saving me from my dread of programming in R, and for helping to transform my clunky methodologies into some slick scripts and a Shiny app.

Thank you to Ruth Brown and to Stefanie Ismar for providing additional blood samples for this PhD. Thanks also to Simon Tollington for helping with the organisation and transport of petrel samples. Claire Raisin developed the petrel microsatellite markers and has patiently provided me with support from afar. Microsatellite development and genotyping was performed at the NERC Biomolecular Analysis Facility (NBAF) at the University of Sheffield and supported by the Natural Environment Research Council (NERC), UK, with the help of Deborah Dawson, Gavin Horsburgh, Rachel Tucker and Andy Krupa. Thanks to Jim Groombridge, Terry Burke and Jinliang Wang for their invaluable expertise and advice on genetic analyses, and to Dada Gottelli for training me to extract museum sample DNA.

I'd like to send a huge thanks to the inspirational Rob Thomas at Cardiff University for first introducing me to petrels during my undergraduate degree. Who'd have thought that eight years and a thesis later, I'd still be so enthusiastic about petrels! I met the legendary Carl Jones through Rob, and Carl gave me my opportunity to spend eight months on Round Island in 2009-2010. It was a tough but incredibly rewarding experience, and I learnt a lot from Rich Baxter, Tom Churchyard and Lucy Rouse.

Hopefully at least some of their toughness rubbed off on me. Thanks to Thalassa McMurdo-Hamilton for being a wizard.

Alex Kirkpatrick has had to weather some dark PhD storms, and has bravely done so without complaint. Thank you for your calm encouragement, patient proof-reading and for constantly amazing me with all your knowledge and terrible puns. To my colleagues, particularly ex-MWFers Gwen Maggs and Helen Gath, thanks for making the sometimes lonely and frustrating PhD world less so and for sharing your own PhD journeys with me. Thanks to Chris Clements for becoming my wise science spirit-guide and unofficial supervisor. Eternal thanks go to Matt Bates and his family for their support in the early days of this PhD; without you I might not be writing this now. To Helen, Kayleigh, Ant, Lea, Scott and Miriam, who have all generously allowed me to sofa-surf with them during this PhD, I'd be much poorer without you! Thanks!

Finally, to my parents: Tim and Diane. I told you many years ago that I wouldn't have a 'Proper Job' till I was thirty, and I'm nearly there! Who knows what the future will bring, but I am sure that you will be there for me, as you always have been. Thank you from the bottom of my heart. This thesis is for you.

Table of Contents

Figures

Tables

Chapter 1: Introduction

1.1 Overview

Seabirds have always captured the imagination of people with their conspicuous colonies and long, enigmatic travels at sea, and have received a great deal of scientific interest. As a result, seabirds are generally well studied at their colonies, but the advent of tracking technology has revealed the extraordinary distances seabirds travel. The discovery of just how wide-ranging pelagic seabirds really are is timely, because seabirds are the second most threatened group of birds globally, after parrots (Croxall et al., 2012, Olah et al., 2016). A number of key threats to seabirds are experienced whilst at sea, chiefly from longline by-catch, pollution, over-fishing, climate change and severe weather (Croxall et al., 2012, Lascelles et al., 2012).

Recent revelations on the at-sea movements of seabirds not only contribute to the conservation of seabirds by informing the creation of Important Bird Areas and Marine Protected Areas (Arcos et al., 2012, Ronconi et al., 2012) but also can provide important information on the location and health of ecologically important areas in the marine environment (Lascelles et al., 2016, Paleczny et al., 2015, Piatt et al., 2007). However, due to the often very inaccessible locations of their colonies, populations of tropical seabirds are frequently overlooked and little is known about their ecology and distributions relative to temperate and polar species.

In many cases even the taxonomy of these tropical species is unclear, making it difficult to assess whether species require conservation action (Mace, 2004, Isaac et al., 2004, Ramos et al., 2016). The genus *Pterodroma* (Gadfly petrels) in the Order Procellariiformes (albatrosses and petrels) has been particularly contentious taxonomically, with species boundaries debated as new genetic techniques are applied to the problem (Zino et al., 2008, Brown et al., 2010, Brown et al., 2011, Brooke and Rowe, 1996, Brooke et al., 2000, Ramos et al., 2016). The difficulty in defining these species is exemplified in the case of the colony of *Pterodroma* petrels on Round Island, off Mauritius in the Indian Ocean (hereafter referred to as 'Round Island petrels'). This population has recently been identified as consisting of three species of *Pterodroma,* with hybridisation and introgression between them (Brown et al., 2011, Brown et al., 2010).

In this thesis, new research is presented which details for the first time current, inter-ocean migration and introgression of tropical *Pterodroma* petrels, focusing on the

unique Round Island population. The pelagic distribution of colony-based Round Island *Pterodroma* is described for the first time using geolocation data and it is demonstrated that the petrels have a high level of variability in their spatial distribution. In light of this variation, the suitability of current seabird density 'hotspot' approaches (Lascelles et al., 2012, Arcos et al., 2012) for use on species with varied distribution patterns is discussed. Finally, possible genetic and environmental explanations for the variation seen in the colony-based distributions of this population are examined and the implications for tropical seabird conservation are discussed.

1.2 Background

Round Island

Located 22.5km off the north-east coast of Mauritius, in the western Indian Ocean, Round Island (19.85º South, 57.78º East) is the flagship conservation project of the Mauritian Wildlife Foundation (MWF), managed in partnership with the Mauritian Government National Parks and Conservation Service (NPCS). Round Island's volcanic origin is clearly evident in its crescent shape (Figure 1); the steep-sided half-crater that remains above the ocean is formed from welded tuff and basalt boulders, and the surface is weathered into overhangs and hollows.

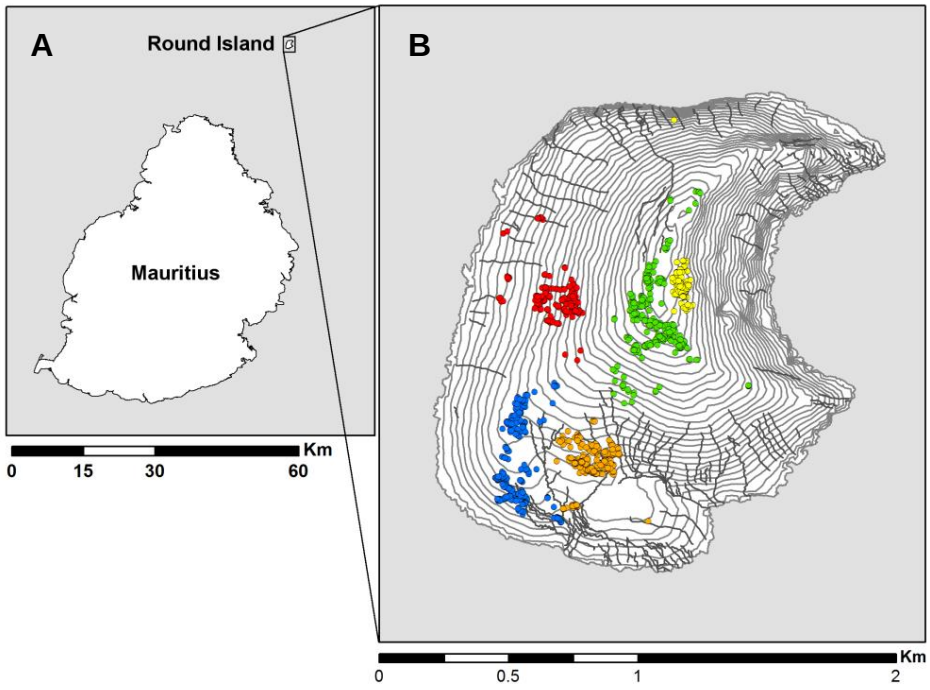

Figure 1: A: Position of Round Island in relation to Mauritius. B: Sub-colonies on Round Island. Coloured points mark known nest sites, clustered into five main groups, colour-coded: blue = 'south-west ridge', orange = 'above camp', red = 'big slab', green = 'summit', yellow = 'crater'.

Miraculously, mammalian predators have never colonised the 214 hectare island, making it one of the largest rodent-free tropical, high islands in the world (BirdLife International, 2016a). As such, it is a haven for seabirds and reptiles alike, and was designated a nature reserve in 1957 (Merton, 1987, Brown, 2008, Tatayah, 2010). Access to the island is restricted to authorised MWF and NPCS staff and researchers, and it is kept strictly quarantined to prevent the introduction of invasive species. The island supports a very large population of seabirds, notably one of the largest colonies of Wedge-tailed shearwaters (*Ardenna pacifica*) in the Indian Ocean, consisting of around 40,000-80,000 pairs, along with 3,000-4,000 pairs of Red-tailed tropicbirds (*Phaethon rubricauda*) and 750-1500 pairs of White-tailed tropicbirds (*Phaethon lepturus*) (Tatayah, 2010). There are two species of petrel uncommonly found at Round Island: three pairs of Bulwer's petrel (*Bulweria bulwerii*) have been discovered nesting at the summit, and non-breeding Black-winged petrels (*Pterodroma nigripennis*) have been observed over several years (pers. obs., Tatayah, 2010).

The unusual case of the 'Round Island' petrel

Interestingly, although the wildlife of Round Island had been documented by several naturalists since 1844 (Brown et al., 2011, Tatayah, 2010, Brown et al., 2010), few petrels were observed on the island until their official documentation by Vinson in 1943 (Brown et al., 2011). The deforestation of Round Island by introduced rabbits and goats, whilst hugely detrimental to the biodiversity of the island as a whole, ironically may have contributed to the colonisation of the island by *Pterodroma* petrels (Brown et al., 2011). The loss of plant life caused by grazing resulted in extensive erosion of the island's topsoil, exposing the bare rock beneath. Since the Round Island petrel population consists of surface-nesting species, this may have increased the number of nest sites available (Brown et al., 2011), assisting their colonisation from outside the Indian Ocean. It is also hypothesised that historically the number of petrels breeding on the island was low due to competition for nest sites with the much larger and more aggressive Red-tailed tropicbirds. The petrel population subsequently may have increased number when Red-tailed tropicbirds were hunted by poachers in the 19th and early 20th centuries (Tatayah, 2010, Cheke and Hume, 2008). Since Round Island became a nature reserve, introduced grazers have been exterminated and seabird poaching has ceased. Unpublished capture-mark-recapture analyses now estimate the population at between 1400-1500 individuals visiting the island annually (M.A.C. Nicoll,

pers. comm.). Due to consistent seabird monitoring by MWF island wardens since 2002 over 95% of the population is now estimated to be ringed.

However they came to arrive at Round Island, since their discovery the petrels have been a source of taxonomic confusion. Specimens collected by Vinson in 1949 were identified by Murphy and Pennoyer (1952) as Trindade petrels. At the time the Trindade petrels were classified as *P. arminjoniana arminjoniana* (now *P. arminjoniana*) and were thought to be an Atlantic race with a smaller Pacific counterpart *P. arminjoniana heraldica* (Herald petrels, now *P. heraldica*). Murphy and Pennoyer (1952) aligned Round Island petrels with Atlantic Trindade petrels primarily due to their similarity in size (Brooke et al., 2000, Murphy and Pennoyer, 1952). Trindade petrels are medium-sized (35-39 cm, Birdlife International, 2016b) gadfly petrels with a highly variable appearance, due to their polychromatic plumage morphs. 'Dark morph' petrels are uniformly dark grey/brown, whereas 'pale morph' Trindade petrels are dark dorsally with white underparts. Intermediates can have either distinct or indistinct delimitations between dark and light feathers, and often appear light brown in colour, possibly due to feather-wear (Tatayah, 2010). The native range of the Trindade petrel is the Atlantic Ocean, where it breeds on the Trindade and Martim Vaz Islands off the coast of Espírito Santo**,** Brazil (population estimate ~ 1130 mature individuals, Luigi et al. 2008 in Birdlife International, 2016b). It is currently classed as 'Vulnerable' on the IUCN Redlist due to its presumed small breeding range and vulnerability to stochastic events (Birdlife International, 2016b).

Later visits to Round Islands by ornithologists began to reveal complications in the supposed species identity of the population. When D.V. Merton visited Round Island in 1986, he identified some birds as giving Kermadec petrel (*P. neglecta*) calls (Brooke et al., 2000), a distinctly different call type to that of Trindade and Herald petrels. Subsequent to this, Brooke et al. (2000) analysed blood samples and phenotypic traits of Round Island petrels, and although they could not distinguish Round Island petrels and Pacific Kermadec petrels using differences in mitochondrial *cytochrome b* genes, they found clear evidence for the presence of Kermadec petrels on Round Island using vocalisations and plumage differences (Brooke et al., 2000).

In appearance, Kermadec petrels strongly resemble Trindade petrels, although often they appear to be larger and slightly bulkier (Tatayah, 2010, pers. obs.). Like the Trindade petrel, they have a plumage polymorphism ranging from dark brown to a pale grey with white underparts, with intermediate colour phases (Murphy and Pennoyer, 1952, Birdlife International, 2016b). The main distinguishing feature that sets the appearance of the Kermadec petrel apart from the Trindade petrel is its characteristic

white primary feather shafts (Figure 2), as opposed to the dark brown of the Trindade petrel.

Figure 2: Characteristic white primary feather shafts of a Kermadec petrel caught at Round Island, 2009. Photo: Katherine Booth Jones.

On Round Island, birds can be found with these white feather shafts or intermediate-coloured shafts, making identification uncertain. Anecdotally (and *pers.obs*), Kermadec petrels are more often heard calling around nest sites at the summit of Round Island (Figure 1, green points), although spatial segregation of nest sites on Round Island has not been researched. The possibility of the Kermadec petrel reaching the Atlantic Ocean has been debated in the literature (Imber, 2004, Imber, 2005, Imber, 2008, Tove, 2005), and despite largely being dismissed, sightings of petrels with the characteristic white primary shafts in the Atlantic have been reported. In the Pacific Ocean the Kermadec petrels have a broad range across the Pacific, stretching across the subtropical Pacific from Lord Howe Island near Australia to the Desventuradas near South America (Brooke, 2004).

The case for the identity of the Round Island petrel was far from closed however. Although at the time the Round Island population was thought to consist of mainly Trindade petrels with some Kermadec petrels, the Round Island population was found to be hosting a single species of *Halipeurus* feather louse, *H. heraldicus* (Brown, 2008, Brown et al., 2011). This louse species was previously only found on the Pacific Herald petrel (*P. heraldica*), whilst Trindade and Kermadec petrels in the Atlantic and Pacific Oceans host a different species, *H. kermadecensis* (Brown, 2008, Brown et al., 2011).

This evidence suggested that *H. heraldicus* had reached Round Island travelling on the feathers of Herald petrels. Prior to the molecular work by Brown et al. (2011), ringing records provided evidence of colony switching and introgression between Pacific Herald petrels and Round Island petrels. A small, pale-plumaged petrel was discovered with a young chick during routine seabird monitoring on Round Island in 2006 (Tatayah, 2010), and was paired with a dark-plumaged Round Island petrel (Brown, 2008). The petrel was identified as a Herald petrel that had originally been ringed as an adult in 1984 at a colony on Raine Island, on the northern tip of the Great Barrier Reef (King and Reimer, 1991). This Herald petrel was recaptured again at Round Island with an egg in October 2008 and in May 2012, at a minimum age of 28 years old, providing proof that petrels can and do colony-switch between the Pacific and Indian Oceans.

As mentioned, Herald petrels were formally considered to be a slightly smaller, Pacific sub-species of *P. arminjoniana* (Murphy and Pennoyer, 1952). However, recent research has split pale phase and dark phase *P. heraldica* into two separate species, the dark phase petrel now belonging to its own species, the Henderson petrel, *P. atrata* (Brooke and Rowe, 1996). The Herald petrel's native breeding range overlaps with that of the Kermadec petrel, and extends from Raine Island off northern Australia to Easter Island in the east (Birdlife International 2015, Brooke, 2004). Analysis of mtDNA haplotypes present at Round Island by Brown et al. (2011) confirmed the presence of Herald petrels at Round Island, and described for the first time the introgression between the Trindade, Kermadec and Herald petrels that breed there.

In their study of Round Island mtDNA haplotypes, Brown et al. (2011) found that also present in the Round Island population were haplotypes not seen in the sampled populations of the three parental species, and posited that these parental populations sampled were incomplete. An alternative to this hypothesis is the potential presence of a fourth species of *Pterodroma* on Round Island. Petrels have been sighted at Round Island resembling Phoenix petrels (*P. alba*), another tropical, Pacific petrel (C. Jones, pers. comm., Tatayah, 2010). The Phoenix petrel bears a strong resemblance to the Herald petrel, but appears more uniform in colouring, compared with the large degree of variation seen in Herald petrel plumage (Murphy and Pennoyer, 1952, Birdlife International, 2016b). The presence of the Phoenix petrel in the Round Island population is plausible given the presence of the three species already confirmed, but so far no strong evidence has been presented. Neither is it clear whether Round Island is unique for its mixed-species population of gadfly petrels. While previous studies have assumed that Round Island represents a point of secondary contact between species of the Atlantic and Pacific (Brooke et al., 2000, Brown, 2008, Brown et al., 2011, Brown

et al., 2010), none have explored the possibility of migration and introgression between *P. arminjoniana, P. neglecta* and *P. heraldica* outside the Indian Ocean.

This thesis therefore aims to firstly improve our understanding of the movement of gadfly petrels between populations. Another important gap in our knowledge of the Round Island petrel is its at-sea distribution. Gadfly petrels are currently extremely under-represented in the literature in this regard, with only a few tracking studies currently published (Rayner et al., 2008, Pinet et al., 2011a, Ramírez et al., 2013, Ramos et al., 2016, Nicoll et al., 2016), and little is known about the distribution of tropical species. This thesis will therefore add to the research available on gadfly petrels by describing the colony-based at-sea distribution of Round Island petrels. Because a relatively large sample size was tracked, I am able explore whether population-level distribution estimates adequately represent the distribution of this population, which is known to be genetically diverse and wide-ranging. Using data previously acquired in Chapters 2-4, the thesis then aims to explore the influence of individual genetic background and environment on petrel distribution during the colony-based period, an area not previously studied in tropical seabirds. Given the great lack of spatial and genetic studies carried out on tropical petrels, this thesis aims to highlight the importance of considering behavioural and genetic diversity in future research.

1.3 Chapter overview and aims

Chapter 2: Widespread gene flow between oceans in a pelagic seabird species complex.

While previous research has identified the presence of three species of *Pterodroma* on Round Island, it is currently unknown whether Round Island presents a unique point of secondary contact between Atlantic and Pacific populations of *Pterodroma*, or whether migration and gene flow between these species is more widespread. The first chapter of this thesis aims to differentiate between two hypotheses that describe the position and significance of the Round Island population in terms of the global populations of Trindade, Kermadec and Herald petrels. For this I use microsatellite genotyping data from petrel samples taken from Round Island and from population of Trindade, Kermadec and Herald petrels from across their ranges. I also include samples from Phoenix petrels to investigate their presence at Round Island, and Murphy's petrel (*P. ultima*) as an out-group. Figure 3 illustrates the two models of gene flow being tested. In the *secondary contact model* (Figure 3A), Round Island is the only island population

that contains migrants from outside the sampled ocean, and their hybrids. Whereas in the *widespread gene flow model*, inter-ocean migrants are found in both the Atlantic and Pacific populations and hybrids between Atlantic and Pacific species are found outside the Indian Ocean (Figure 3B).

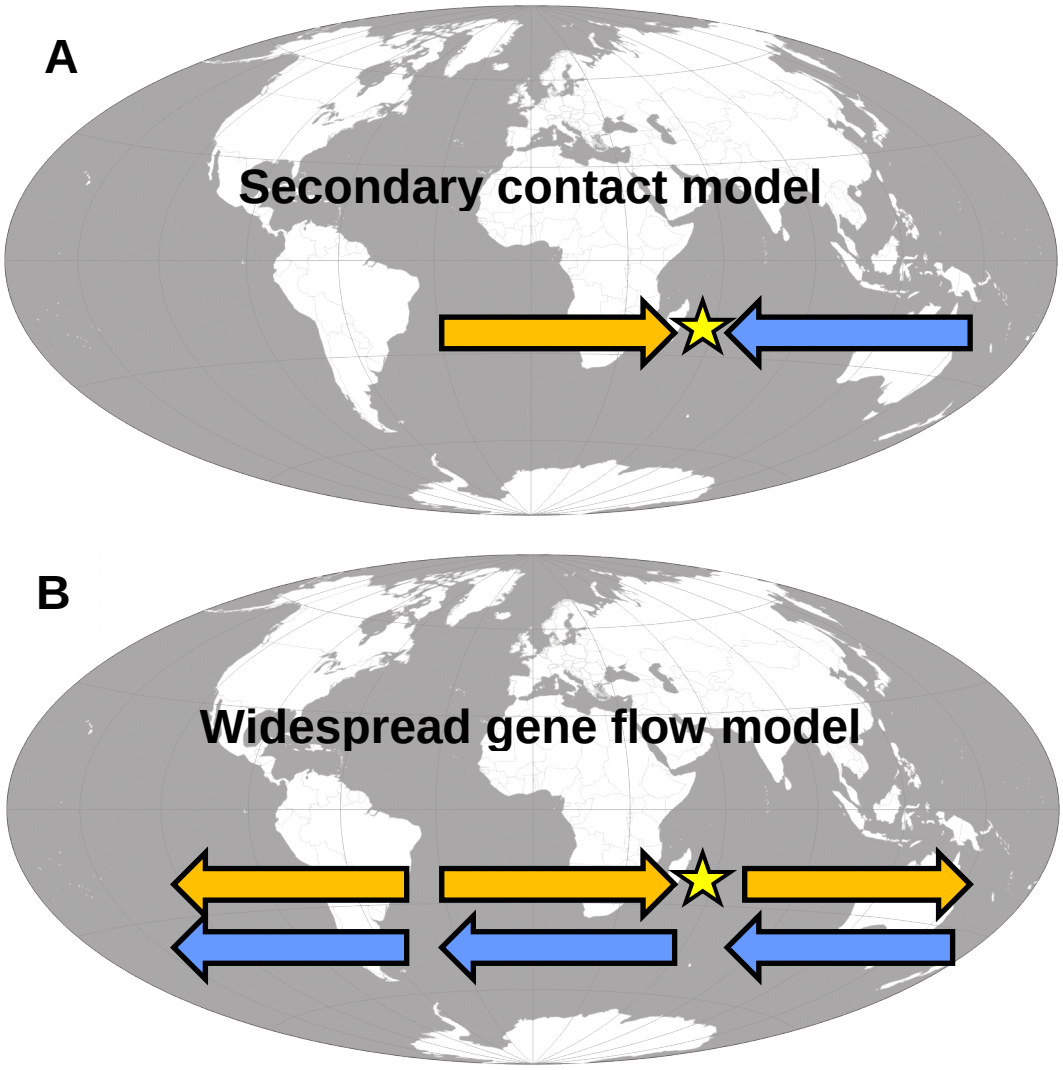

Figure 3: The two hypotheses of petrel gene flow between Round Island and populations in the Atlantic and Pacific Oceans. Orange arrows represent the movement of Trindade petrels (*P. arminjoniana*) from the Atlantic Ocean, and blue arrows represent the movement of Kermadec and Herald petrels (*P. neglecta* and *heraldica*) from the Pacific Ocean.

The Round Island petrel population presents a unique system in which to explore the relationship between dispersal ability and sympatric barriers to gene flow, because like all seabirds, they have incredible potential for dispersal and interbreeding between different colonies, but show a range of behaviours that prevent this (Friesen, 2015). Round Island represents the only well-studied example of a naturally occurring three-way hybrid seabird population in the world. Studying gene flow between oceans in this population therefore has interesting conservation implications, particularly given the

threatened status of seabirds globally (Croxall et al., 2012). In conservation planning, it is useful to be able to differentiate populations into defined compartments, be that into species, or pockets of genetically valuable populations, before levels of risk can be calculated or conservation management plans can be devised (Isaac et al., 2004, Mace, 2004). However, in reality species are not so rigidly defined. In a Darwinian sense, species are part of an evolutionary continuum through space and time (Isaac et al., 2004) and boundaries between them are constantly in flux. In particular, dispersal and gene flow between populations, or even species, may work counter to this neat compartmentalising of populations into distinguishable units. When there is incomplete physical separation between closely related taxa, gene flow between the groups may still occur (Nosil, 2008), which in most cases opposes the segregation of these groups into distinct species (Garant et al., 2007, Smadja and Butlin, 2011). Understanding this balance provides an insight into the evolutionary past and future of populations, and as such is an important consideration for conservation ecology (Genovart et al., 2013).

In Chapter 2, I highlight how little is known about the potential for wide-ranging dispersal and introgression between closely related *Pterodroma*, and discuss how this may affect the future of vulnerable populations.

Chapter 3: An approach for recovering degraded geolocation data in animal tracking studies.

Understanding animal movement and distribution is fundamental to ecology, and as with many tropical seabirds, nothing is currently known about the at-sea distribution of Round Island petrels. An increase in the use of tracking technology has enabled researchers to reveal the pelagic distributions of many species, and this is particularly exciting in wide-ranging Procellariform seabirds. Global Location Sensors (GLS), more commonly known as ‘geolocators’ are popular archival tags due to their low cost, enabling researchers to track a large numbers of their study species. However, geolocation relies on the uninterrupted recording of sunrise and sunset events, and false shading of the geolocator during daylight hours by the host or habitat can result in the generation of inaccurate locations. Shading by the host is particularly problematic in surface nesting seabird species, such as the Round Island petrels, as it is conventional to attach geolocators to the leg of the bird. When the petrel lands on the island, it sits and covers the light sensor intermittently, causing shading noise in the recorded light data. I found that for my analysis, this interrupted light recording caused varying

degrees of error in the location estimates and in cases with extensive shading, caused the geolocation model to fail.

Previously, geolocation studies have used manual methods to reduce daytime shading noise in their data. These require the user to judge all transitions between light and dark to decide whether they are useable for further analysis or falsely generated, and discard degraded data accordingly. Understandably this process is subjective, extremely time-consuming and unlikely to be repeatable. In Chapter 3 I develop a novel approach to eliminate interference caused by daytime shading noise in geolocation data, greatly speeding up and standardising the geolocation process, and demonstrate its use on data from the Round Island petrel population.

The new approach, '`CleanLight`', allows the user to systematically clean degraded light data, using either automated R scripts, or a user-friendly, Shiny web application. This novel approach to recovering degraded light data contributes to the standardisation of geolocation analysis, by minimising observer bias and thus increasing the repeatability of results. For large studies, the time-saving automation may be particularly beneficial. Due to the widespread use of geolocators, this work will be useful to researchers in a diverse range of fields including conservation, ecology, and demography. In this thesis, it enables me to study for the first time the colony-based distribution of Round Island petrels using cleaned geolocation light data.

Chapter 4: The importance of quantifying intra-population variation in the at-sea distribution of colony-based seabirds when identifying marine hotspots.

Marine areas that are valuable to seabirds are likely to be areas of high biological activity (Durant et al., 2009) and therefore important areas to conserve for other marine taxa also. By tracking seabirds to the areas they use at sea, areas of ecological importance for seabirds and other marine life can be identified and potentially conserved.

Whilst seabird breeding colonies are traditionally well studied and may be afforded protection, pelagic foraging areas around the colony are less likely to be protected (Grecian et al., 2012) and are critical to the breeding success of the population (Thaxter et al., 2012, Maxwell and Morgan, 2013). Identifying these areas in not straightforward, as not all individuals in a population may use the same foraging locations around their breeding colony. For tropical species particularly, where prey

availability is more patchy and unpredictable than in temperate and polar biomes (Jaquemet et al., 2007, Monticelli et al., 2007, Hennicke and Weimerskirch, 2014), intra-population plasticity in foraging behaviour may be an advantage. However, compared with temperate and polar species, tropical seabirds remain under-represented in the literature.

Many studies use tracking technology to identify important foraging areas for seabird colonies. However, until recently few studies have looked for intra-population differences in the foraging areas seabirds use during this crucial stage of their life cycle. This gap in our knowledge of seabird behaviour may be due to insufficient sample sizes in previous studies, but with the ever decreasing cost of trackers, the study of intra-population variation is on the rise.

When investigating variation in a population, many studies divide the population *a priori*, e.g. by sex (Pinet et al., 2012a, Weimerskirch et al., 2009) or by species (Weimerskirch et al., 2009, Kappes et al., 2011, Young, 2010) before comparing distributions between individuals, and this may potentially introduce observer bias. Rather than using this approach, in Chapter 4 I divide the ocean around Round Island into regions that are then used to differentiate foraging distributions of petrels using space alone using a bespoke Bayesian Mixtures Analysis. I compare the areas identified using this method to areas identified without looking for intra-population variation and find that population-level estimates are inadequate to describe the area of use around the colony for Round Island petrels.

This study is the first of its kind to look at individual variation in the colony-based, at-sea distribution of tropical petrels, demonstrating that even during the restrictive colony-based period petrels do not all behave in the same way. The adequate representation of variation is particularly important when considering marine hotspots for protection, as intra-population behavioural plasticity is essential to sustaining populations in increasingly changeable future conditions.

Chapter 5: Colony-based distribution of tropical petrels influenced by seasonal climate, but not genotype.

In Chapter 4 I describe for the first time the distribution of Round Island petrels around their colony, and show that the population demonstrates considerable intra-population variability. Due to this, Round Island petrels provide an unusual opportunity to explore the influence of both genetic and environmental factors on colony-based distribution. In

Chapter 5 I investigate whether variations in Round Island petrel distributions are due to individual differences based on ancestral genotypes or the influence of seasonal environmental change.

As previously discussed, the Round Island population consists of at least three different species of *Pterodroma* petrel, originating from difference oceans. There is precedent to suggest that species differences may cause variation in foraging distribution in *Pterodroma* petrels. Notably, a recent study on Atlantic Ocean petrels breeding on the Macaronesian islands of Madeira (Zino's petrel, *Pterodroma madeira*), Desertas (Desertas petrel, *P. deserta*) and the Cape Verde archipelago (Cape Verde petrel, *P. feae*) found that the different species displayed spatio-temporal segregation in their distributions during both the breeding and non-breeding periods (Ramos et al. 2016). This is thought to be one mechanism that reduces gene-flow between closely related species (Friesen et al. 2007a, Friesen 2015). In addition, differences in foraging distribution between species at a colony can reduce competition for resources (Ashmole 1963, Lewis et al. 2001), which may be a particular constraint for tropical species breeding in oligotrophic areas. For example, different species in a community may specialise in different prey types and or visit particular areas (Hyrenbach et al. 2002, Pinaud & Weimerskirch 2007, Weimerskirch et al. 2009, Navarro et al. 2009d, Young 2010, Kappes et al. 2011, Navarro et al. 2014, Young et al. 2015), resulting in variations in at-sea distributions around the colony.

Round Island petrels may also be influenced by seasonal changes in the marine environment, which in turn affect prey availability around the island. Unlike in temperate or polar climates where a particular time of year may have a superabundance of prey, tropical regions lack strong, seasonally predictable prey resources and are characteristically low in productivity and prey abundance (Ashmole 1963, Ashmole 1971, Ballance & Pitman 1999). Due to this, tropical seabirds (Round Island petrels included) often have protracted or asynchronous breeding cycles and as such are exposed to weak seasonal differences at the colony throughout the year. Tropical seabirds have been demonstrated to have flexible foraging distributions, which is likely to be an adaptation to oligotrophic and unpredictable oceans (Pinaud & Weimerskirch 2005b, Weimerskirch 2007, Burke & Montevecchi 2009, Deppe et al. 2014).

On Mauritius, in the south-western Indian Ocean, the year can be divided into two broad seasons: the austral winter (May-late September) and the austral summer (October - late April) (Jury & Pathack 1991, Le Corre 2001, Staub et al. 2014), linked to the monsoon circulation of the Indian Ocean. Seasonal changes in the marine conditions of the area, namely lower sea surface temperatures and higher chlorophyll *a*

concentrations in the winter (Le Corre 2001, Wiggert et al. 2006) are expected to influence prey abundance around Round Island (Lévy et al. 2007). Since Round Island petrels have an asynchronous breeding cycle, individual petrels with different annual schedules will be exposed to a range of seasonal conditions, and therefore may have different distributions in response to changes in prey availability between the seasons.

Finally in Chapter 5, I bring together the elements of the previous chapters to test the influence of seasonal change and individual membership to a parental species group on the distribution patterns of Round Island petrels using a multinomial logistic regression approach.

Chapter 6: Discussion

In Chapter 6 I conclude my thesis by summarising the new knowledge that has resulted from each of my data chapters and discuss their implications for both the Round Island petrel and seabirds as a whole. I consider the gaps in our current knowledge and explore possible directions for future research.

Summary

Seabird populations are in decline globally (Croxall et al., 2012), and *Pterodroma* petrels are one of the most threatened and least studied seabird taxa (Ramos et al., 2016). This thesis aims to provide a valuable and timely first look at the connectivity of petrel populations and how their varied, wide-ranging lifestyles are influenced by their genes and their environment.

Chapter 2: Widespread gene flow between oceans in a pelagic seabird species complex

2.1. Abstract

Although seabirds are capable of dispersing across vast distances, they exhibit a number of evolved and behavioural traits that limit gene flow. Whilst many studies focus on the gene flow between single species at different colonies, the potential for gene flow and introgression between species is understudied, particularly in Procellariiformes. The only well studied example of a mixed species, hybridising population of petrels exists on Round Island, in the Indian Ocean.

Previous research suggested that Round Island is a point of secondary contact between Atlantic (*Pterodroma arminjoniana*) and Pacific species (*P. neglecta* and *P. heraldica*). However, the possibility of dispersal and gene flow occurring outside the Indian Ocean has not been addressed. This study uses microsatellite genotyping and tracking data to differentiate between two hypotheses describing gene flow involving the Round Island *Pterodroma* population: the *secondary contact model* and the *widespread gene flow model*.

Dispersal and introgression spanning three oceans was demonstrated between species in this complex. Analysis of migration rates estimated using BAYESASS revealed unidirectional movement of petrels from the Atlantic and Pacific into the Indian Ocean. Conversely, STRUCTURE analysis revealed migration and admixture of species occurring between the Atlantic and Pacific Oceans, with potential three-way hybrids occurring outside the Indian Ocean. Additionally, geolocation tracking of Round Island petrels revealed two individuals travelling to the Atlantic and Pacific, before returning to breed on Round Island. Results of these analyses suggest that inter-specific hybrids in *Pterodroma* petrels are more common than was previously assumed and support the *widespread gene flow model*.

This study is the first of its kind to investigate migration and gene flow between populations of closely related Procellariform species on a global scale, and has important implications for the conservation and taxonomy of other widely dispersing species.

2.2. Introduction

Seabirds provide a particularly interesting model in which to examine evolutionary genetics and the relationship between dispersal and gene flow, due to the dichotomy between their huge potential for dispersal coupled with their reluctance to do so, driven by a strong instinct for philopatry (Steeves et al., 2005, Friesen et al., 2007a). With an almost unlimited potential for dispersal, panmixia between closely related species or subspecies would be the expected outcome. However the preference of seabirds to return to their natal island to breed can lead to island populations becoming distinct (Abbott and Double, 2003, Austin et al., 1994, Avise et al., 2000, Burg and Croxall, 2001). Although natal philopatry does not always result in population differentiation between islands (Milot et al., 2008, Ando et al., 2011, Dearborn et al., 2003, Gómez-Díaz et al., 2009, Morris-Pocock et al., 2010), other sympatric barriers to gene flow in seabirds, such as non-breeding distribution (Burg and Croxall, 2001, Morris-Pocock et al., 2010) or adaptation to local ocean regimes leading to ecological speciation, may also play an important role in dividing seabird populations (Schluter, 2009, reviewed in Friesen, 2015, Gómez-Díaz et al., 2009).

Whilst many studies focus on the gene flow and genetic structure between single seabird species at different island colonies, the potential for gene flow between different species at different spatial scales remains poorly understood (Friesen, 2015). Introgression between bird species is fairly common in nature (Mallet, 2005, Grant and Grant, 1992, McCarthy, 2006), but is usually prevented by biological or physical barriers. It has been demonstrated that gene flow between conspecific populations of seabirds is often restricted (Friesen, 2015) and therefore introgression of genes from one seabird species to another through the movement of individuals to different breeding colonies may be considered very unlikely.

However on Round Island, off the coast of Mauritius in the south-western Indian Ocean, there is an unusual colony of *Pterodroma* petrels. The population includes three species (Trindade petrel, *P. arminjoniana,* Kermadec petrel, *P. neglecta* and Herald petrel*, P. heraldica*), known to extensively hybridise here (Brown et al., 2011, Brown et al., 2010). The only other breeding location of the Trindade petrel is in the South Atlantic at the Trindade and Martim Vaz archipelago (Brooke, 2004). Unlike the population of the Indian Ocean, in their Atlantic range Trindade petrels have no confirmed contact with Kermadec or Herald petrels, although the possible presence of Kermadec petrels in the Atlantic Ocean has been debated and largely dismissed due to insufficient evidence (Imber, 2004, Imber, 2005, Imber, 2008, Tove, 2005). In contrast,

in the Pacific ocean Kermadec and Herald petrels share a similar range, and several breeding locations (Brooke, 2004, BirdLife International, 2016c). Despite the overlapping Pacific range of Kermadec and Herald petrels, they are not known to hybridise in the Pacific. The petrel population on Round Island therefore represents a particularly interesting 'natural experiment' in which to study the role of dispersal, gene flow and the breakdown of barriers between species that are both formally allopatrically and sympatrically separated. The potential for inter-ocean gene flow between the species involved in the Round Island *Pterodroma* complex has important conservation implications for wide-ranging species such as pelagic seabirds, and also for our understanding of evolution at large spatial scales in an ever-changing marine environment.

Here a combination of microsatellite genotyping and geolocation tracking data is used to distinguish between two potential models of gene flow involving the Round Island *Pterodroma* population. In the past, it has been presumed that Round Island is a point of secondary contact between Atlantic and Pacific species. In the *secondary contact model*, gene flow only occurs from the Atlantic and Pacific to Round Island, and therefore co-occurrence of Atlantic and Pacific species and their hybrids should only occur on Round Island. However, given the huge dispersal potential of *Pterodroma* petrels, it is possible that the *widespread gene flow model* may be true. In this scenario, Atlantic and Pacific species and their hybrids may co-occur on islands other than Round Island, outside the Indian Ocean. Given the historical evidence that *Pterodroma* petrels disperse between oceans, the possibility of introgression of Trindade petrels into the Pacific Ocean and Pacific species into the Atlantic is investigated in this chapter. By genotyping island populations across the Atlantic, Indian and Pacific Oceans, I aim to distinguish between the two potential models of gene flow.

2.3. Method

Monitoring and tracking of Round Island Petrels

Since 1994, petrels have been routinely ringed on Round Island Nature Reserve (19.85° south; 57.78° east, Figure 4) and between 2009 and 2012 330 petrels were fitted with geolocation trackers. For details on ringing and geolocation tagging, see Appendix A.

Sample Collection and DNA extraction

Blood samples were collected from Round Island *Pterodroma* (hereafter referred to as 'Round Island petrels'), Trindade petrels from the Trindade Islands and from Kermadec petrels from the Kermadec Islands (Table 1, Figure 4). Due to the inaccessible nature of many of the islands in the Pacific range of tropical *Pterodroma*, blood samples were unavailable, so to represent the Pacific ranges of the study species footpad tissue was sampled from the American Museum of Natural History's collection. In addition to Herald and Kermadec petrels, Brown *et al*., (2011) posited that there could be additional *Pterodroma* species reaching Round Island from the Pacific. To investigate this, samples from Phoenix (*P. alba*) petrels were also collected, since there have been sightings of petrels with Phoenix petrel-like plumage (having a uniform brown underwing) at Round Island. Additionally, samples from two island populations of Murphy's petrel (*P. ultima*), another tropical Pacific gadfly petrel (phenotypically less similar than the other species) were included as an out-group for genotyping (Table 1, Figure 4). For details of sample collection and storage, see Appendix A. DNA extractions for blood and museum samples were carried out in separate labs using standard procedures, detailed in the Appendix A.

Table 1: Number and origin of petrel samples. N_S = Number of samples, N_G = Number genotyped at >75% of 12 microsatellite markers.

Putative species	**Geographic location**	**Region**	**N_S**	**Type**	**N_G**
Unknown	Round Island	Indian Ocean	561	blood	484
Trindade petrel (*Pterodroma arminjoniana*)	Trindade Islands	Atlantic Ocean	52	blood	45
Herald petrel (*Pterodroma heraldica*)	Ducie Atoll	Pacific Ocean	30	museum	28
	Marquesas Islands	Pacific Ocean	23	museum	23
	Oeno Island	Pacific Ocean	21	museum	21
Kermadec petrel (*Pterodroma neglecta*)	Ducie Atoll	Pacific Ocean	30	museum	25
	Juan Fernandez Islands	Pacific Ocean	30	museum	28
	Kermadec Islands	Pacific Ocean	29	museum	29
	Kermadec Islands	Pacific Ocean	41	blood	24
	Rapa Island (Bass Islands)	Pacific Ocean	30	museum	29
Murphy's petrel (*Pterodroma ultima*)	Marotiri Island	Pacific Ocean	28	museum	26
	Oeno Island (Bass Islands)	Pacific Ocean	30	museum	30
Phoenix petrel (*Pterodroma alba*)	Christmas Island (Kiritimati)	Pacific Ocean	30	museum	30
	Pitcairn Islands	Pacific Ocean	21	museum	18
	Marquesas Islands	Pacific Ocean	29	museum	29
	Phoenix Islands	Pacific Ocean	16	museum	16
Total			1001		885

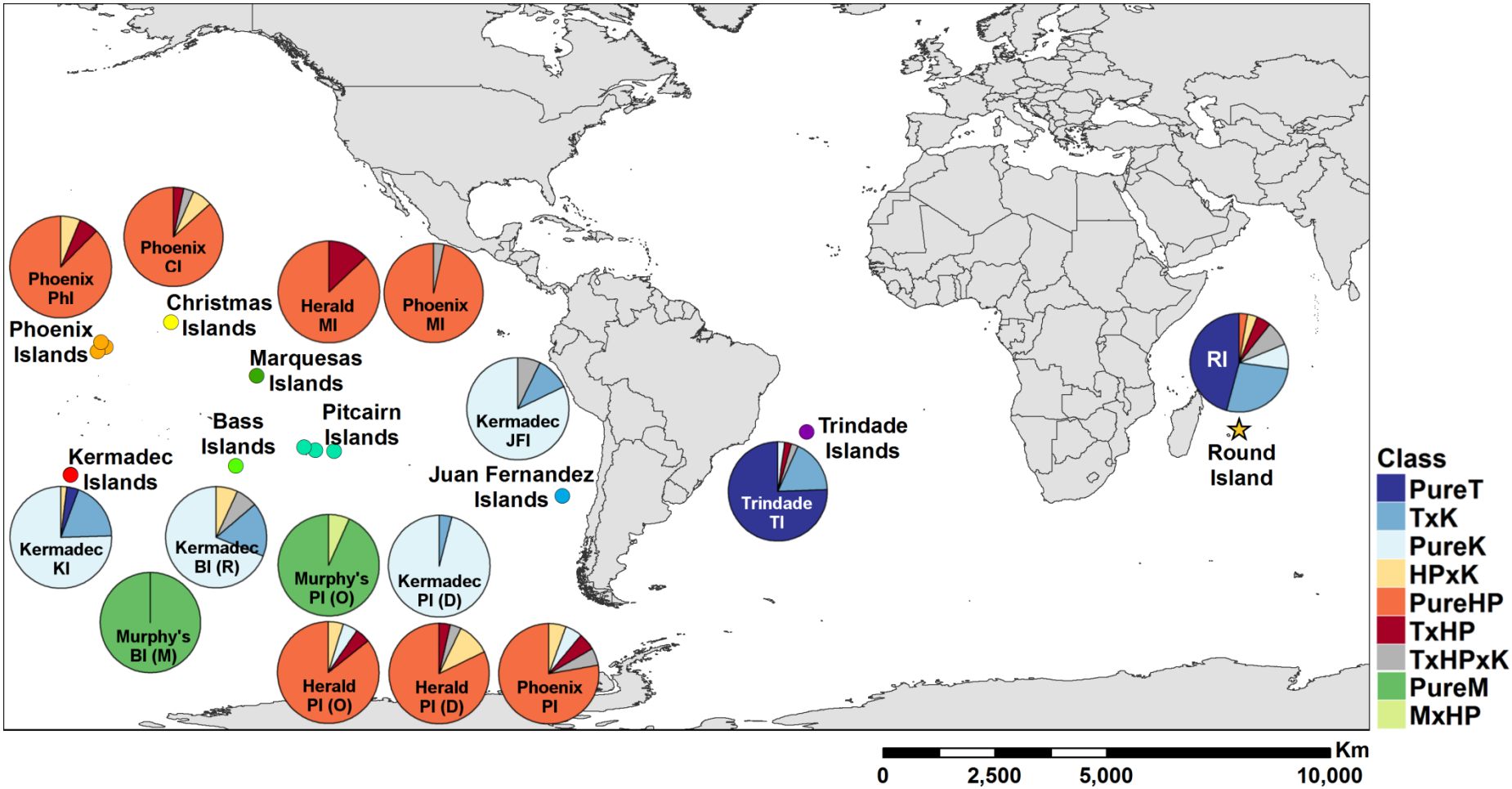

Figure 4: The global distribution of islands sampled. West to east, KI = Kermadec Islands, PhI =Phoenix Islands, CI = Christmas Islands, BI (R) = Bass Islands- Rapa Island, BI (M) = Bass Islands- Marotiri, MI = Marquesas Islands, PI = Pitcairn Islands, all, PI (O) = Pitcairn Islands- Oeno, PI (D) = Pitcairn Islands- Ducie, JFI = Juan Fernández Islands, TI = Trindade and Martim Vaz Islands, and Round Island (orange star). Pie charts represent individuals grouped by recorded species at sampling time and source-island the sample originated from. The class assignment of petrels in each pie chart is derived from estimated membership to each of the four potential clusters identified using STRUCTURE analysis (Table 7, Appendix A).

DNA amplification, genotyping and testing

Two di- and tetra-nucleotide repeat enriched genomic libraries were created from blood samples from one *P. arminjoniana* from the Trindade Islands and one *P. heraldica* from the Gambier Islands. From the libraries, 11 validated microsatellite loci (five from *P. arminjoniana* and six from *P. heraldica*) were chosen that amplified in the three focal species: *P. arminjoniana*, *P. neglecta* and *P. heraldica* and showed some specificity between species. The genetic diversity of these markers was tested between study species to look for evidence of ascertainment bias (Ellegren et al., 1995) (Appendix A). In the final marker set, the following loci were also shown to have cross species utility and were consequently also included; *TG03-002*, *TG13-009*, *TG13-017* (Dawson et al., 2010) , *Tgu06* (Slate et al., 2007) and *Calex01* (Küpper et al., 2007), giving a total of 16 loci. Further details of library development and microsatellite loci used can be found in Appendix A. DNA was amplified using Qiagen Multiplex PCR kits and a touchdown PCR cycle, the conditions of which can be found in Appendix A. Estimates of null allele frequency and tests of Hardy-Weinburg Equilibrium and genotyping error were carried out at each loci within species groups (Table 5, Appendix A).

Estimation of genetic differentiation

Genetic differentiation between populations was investigated using two approaches; using genetic variance between island populations of the species and by looking for population structure across the dataset. F_{ST} (the proportion of the total genetic variance found in the sub-population) calculations were performed using FSTAT to describe genetic variance between island populations. Additionally, F_{ST} was calculated to quantify the genetic difference between the historical Kermadec petrel samples from the Kermadec Islands and the contemporary samples of the same species and location, to investigate whether there was a possible effect of genetic drift between the historical samples and the contemporary samples. Population structure across all samples was estimated using the clustering software STRUCTURE v.2.3.4. (Pritchard et al., 2000, Falush et al., 2003). Details of STRUCTURE analysis can be found in Appendix A.

Hybrid classification

Petrels were assigned to one of nine possible ‘classes’ based on their estimated membership (*Q*) to clusters identified using STRUCTURE analysis (Figure 17). Classes

distinguished individuals likely to belong solely to a particular species group or to a hybrid of two or more groups, with thresholds based on Vähä and Primmer (2006) and Marie et al. (2011). Table 7 in Appendix A describes the criteria used to assign individuals to a particular class.

Estimation of migration

Gene flow was estimated using the software BAYESASS v3.0.3. (Wilson and Rannala, 2003, Rannala, 2012). Based on preliminary STRUCTURE results, Murphy's petrel was not included in analyses of gene flow, as the analysis suggested these populations were not exchanging individuals with other populations. Mixing parameters were adjusted in preliminary runs to ensure that the acceptance rate fell between 20% and 60% and that adequate parameter space was sampled (Beerli, 2009, Beerli and Felsenstein, 2001), to 0.15, 0.40 and 0.60 for migration rate, allele frequency and inbreeding coefficients, respectively. Following Davy et al. (2015), ten separate analyses were run using different random starting seeds. Each run had 2.5×10^7 iterations and a 1.5×10^7 burn-in, and the default sampling interval of 2000 iterations. The optimal run of the ten was identified using Bayesian deviance calculated using an R-script developed in Meirmans (2014), and the mixing parameters and starting seed for this run were used in a final, longer run with 10^8 iterations and a burn-in of 10^7. To investigate the role of Round Island as a possible stepping stone for introgression or point of secondary contact between populations of the Atlantic and Pacific Oceans, the analysis was also run, using the same parameters as above, without the Round Island samples, as seen in Davy et al. (2015).

2.4. Results

The results of investigating null allele frequency, Hardy Weinburg equilibrium, genotyping error for the loci used in this study can be found in Appendix A, along with the results of testing for evidence of ascertainment bias by the calculation of genetic diversity between the species.

Analysis of genetic difference between the island populations of petrels using F_{ST} revealed that most were significantly differentiated, with only seven out of 105 island population pairs being non-significantly different (Table 8). Of these seven comparisons, the majority (five) were between island populations of the same species. However, Phoenix petrel samples collected from the Pitcairn Islands were not

significantly differentiated from two Pitcairn Island-populations of Herald petrels: Herald petrels from Ducie Atoll (F_{ST} = -0.01, P = 0.56), and from Oeno Island (F_{ST} = 0.01, P = 0.24). Comparison between the museum sampled Kermadec petrels from the Kermadec Islands (1920s) and those collected recently (Brown et al., 2011) demonstrated there was no significant genetic differentiation between the temporally separated populations (F_{ST} = 0.004, P = 0.10).

The most likely number of genetic clusters in the dataset using STRUCTURE was found to be four, and these appeared to describe Trindade-type petrels, Kermadec-type petrels, Herald- or Phoenix-type petrels and Murphy's-type petrels (Figure 17). Herald and Phoenix petrels across their ranges were both assigned to the same cluster. Estimated membership (*Q*) to each of these clusters was used to assign individuals to either a 'pure' species, based on the four possible clusters, or a hybrid of two or more species groups. As might be expected with the STRUCTURE clusters largely adhering to species distinctions, Trindade-type individuals were characteristic of the Atlantic Ocean, whereas Kermadec-type, Herald/Phoenix-type and Murphy's-type were characteristic of the Pacific. The proportion of individuals in each class for island populations is shown in Figure 4. Round Island was the most admixed population, with 43.2% of individuals assigned to more than one cluster. Admixture between clusters was not unique to Round Island however; of the other islands sampled Kermadec petrels from Rapa Island (31.0%) and the Kermadec Islands (20.8%) and Trindade petrels from the Trindade Islands (22.2%) also had high levels of split-assignment to clusters, with 24.1%, 18.9% and. 22.2 % (respectively) of each population appearing to be hybridised with a cluster originating from a different ocean to that of the island. Two individuals sampled from the Kermadec petrel population of the Kermadec Islands were classified as belonging to the Trindade-type species cluster, and one individual from the sampled Trindade petrels of the Atlantic Ocean was classified as a Kermadec-type. Of the 885 petrels genotyped globally, 48 had a three-way split assignment between the Trindade, Kermadec and Herald-Phoenix cluster, of which 39 originated from Round Island.

Estimates of migration rates between island populations of Trindade petrels, Kermadec petrels, Herald petrels, Phoenix petrels and the mixed Round Island population are described fully in Table 9 and Table 10 in Appendix A. Significant migration rates are illustrated by Figure 5. No significant migration was calculated from Round Island to other islands, in either the Atlantic or Pacific Oceans, whereas there was significant movement from Trindade (18% ± 0.04% of Round Island individuals per generation), Herald (Marquesas Islands, 1% ± 0.01%) and Kermadec (Kermadec Islands, 5% ±

0.01%) to Round Island. When Round Island was removed from the analysis, no significant migration was seen between the Atlantic and Pacific populations.

Only two individuals (~1% of successfully tracked with geolocators) left the Indian Ocean (Figure 6). In February 2010 petrel 5H41524 left Round Island and travelled eastwards into the Pacific Ocean. Here it travelled close to the nearest colony of known Kermadec petrels on Lord Howe Island and also close to Raine Island (Figure 6), where Herald petrels are known to breed. The petrel was recovered with the geolocator on Round Island on 12th November 2012. Unfortunately no genotyping information was available for the 5H41524, although phenotypically this bird resembled a Kermadec petrel as it was comparatively large and pale in plumage, with characteristic pale primary shafts. In contrast, petrel 5H41919 departed Round Island on 2nd October 2012 and remained within the Indian Ocean until it passed around the southerly tip of Africa and travelled into the Atlantic Ocean, close to the Trindade and Martim Vaz archipelago, the Atlantic breeding site of the Trindade petrel. The petrel is subsequently recaptured on Round Island on 1st June 2013 (Figure 6). Petrel 5H41919 was assigned predominantly to the Kermadec cluster (61.9%) but also to the Trindade cluster (28.7%), and had a low assignment to the Herald/Phoenix cluster (7.7%) and Murphy's cluster (1.7%).

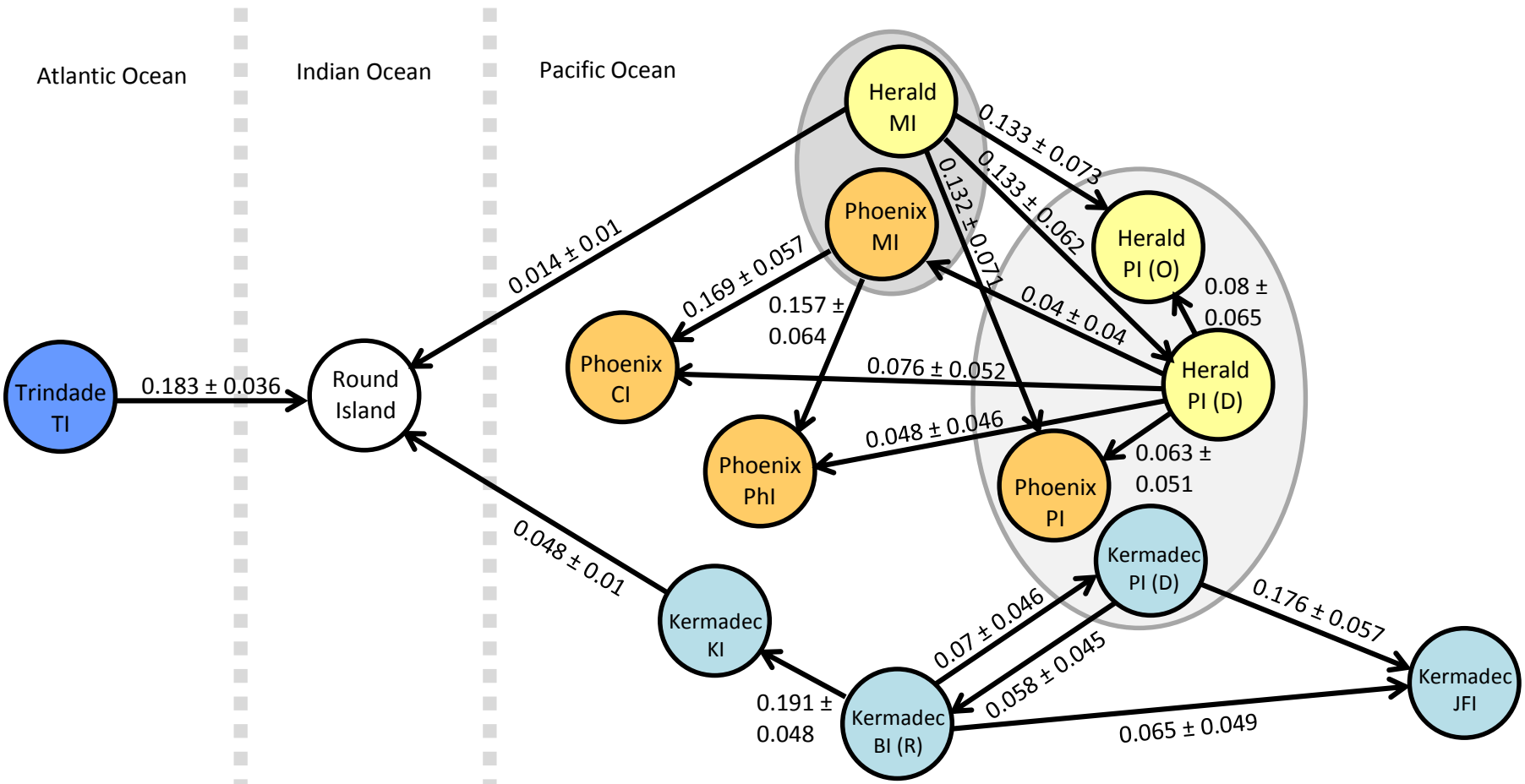

Figure 5: Migration rates (proportion of migrants from population x in population y per generation) between island populations, ± confidence intervals (1.96 x the standard deviation, as in Rannala (2012)). For example, 0.183 (18%) ± 0.036 of the Round Island population originates from the Trindade petrel population per generation. Black arrows represent the direction of movement. Dotted lines indicate divides between oceans. The dark blue circle represents the Trindade petrel population of the Trindade Islands, light blue circles are Kermadec petrel islands, yellow circles are Herald petrel islands and orange circles are Phoenix petrel islands. Grey background circles represent populations from the same island group: dark grey = Marquesas Islands, light grey = Pitcairn Islands. Island abbreviations are the same as in Figure 4.

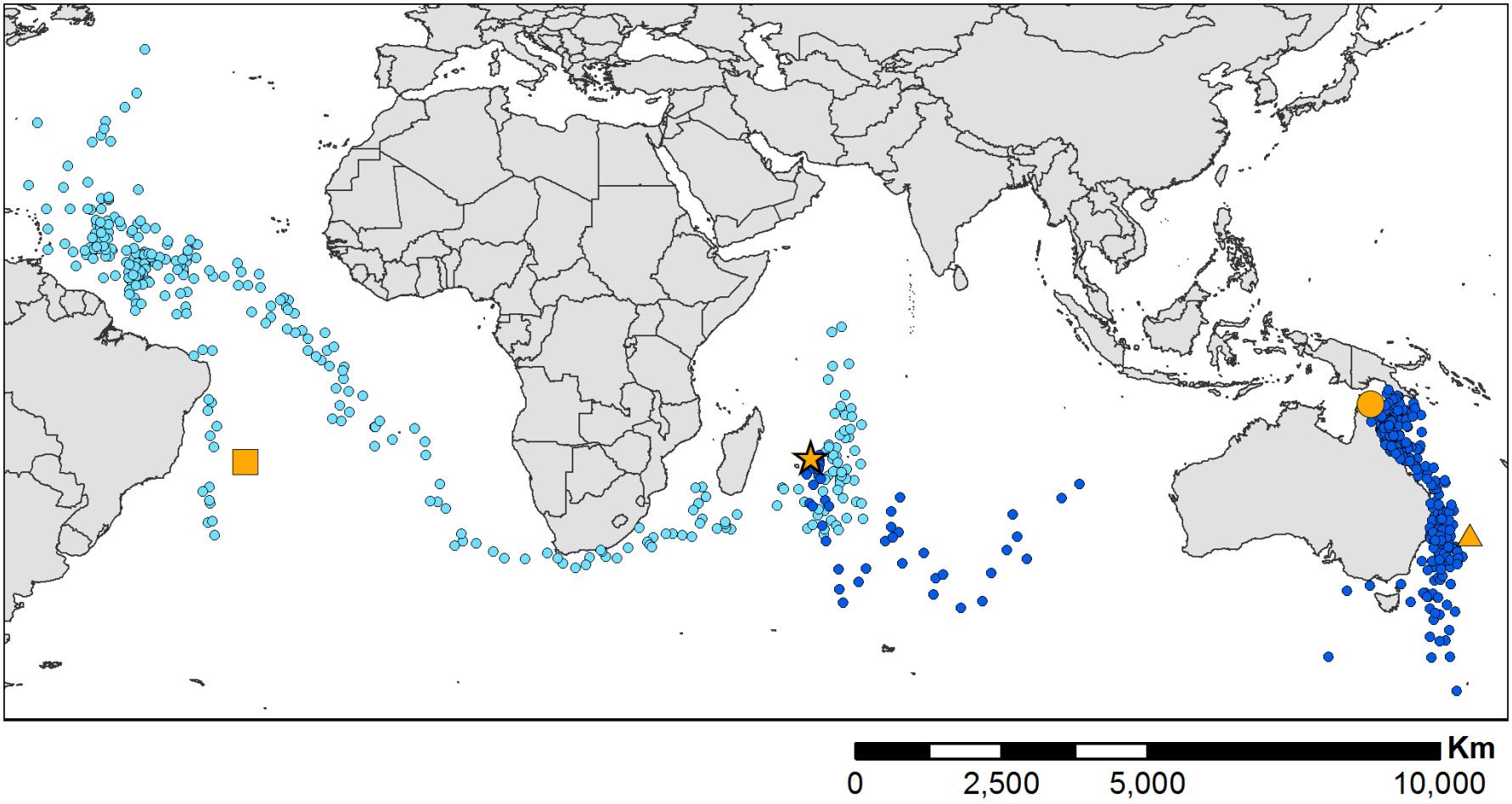

Figure 6: Recorded movement of individuals between oceans. Two individual petrels fitted with geolocators that departed from Round Island in the Indian Ocean and migrated into the Atlantic and Pacific Oceans. Light blue points represent locations from petrel 5H41919 (female) between 02/10/2012 - 11/03/2013. Dark blue points represent locations from petrel 5H41524 between 19/02/2010- 18/08/2010. Orange star = Round Island. Orange square = Trindade Islands (Brazil), the only other known colony of the Trindade petrel. Orange circle = Raine Island (Australia), where Herald petrel 061-39302 was ringed before it subsequently was found breeding on Round Island between 2006 – 2012 (see Discussion). Orange triangle = Lord Howe Island, the closest known Pacific Kermadec petrel colony to Round Island.

2.5. Discussion

This study presents for the first time evidence for the exchange of individuals between species of Procellariform seabird across different oceans. Analysis of microsatellite genotyping data using STRUCTURE found that within the five species sampled across three oceans, four clusters best represented the population structure between these groups, and these corresponded largely to the species studied. The population of petrels on Round Island was shown to consist mainly of individuals belonging to the Trindade-type cluster, however levels of admixture between Kermadec and Herald-type clusters were higher on Round Island than in the other island populations sampled (Figure 4). Significantly, admixture between clusters was also seen outside the Indian Ocean, in the Trindade petrel population of the Atlantic Ocean and Kermadec, Herald and Phoenix petrel populations of the Pacific, providing strong evidence of dispersal and gene flow outside the Indian Ocean. Analysis of per-generation migration rate using BAYESASS recorded significant migration rates into the Round Island population from the Trindade, Kermadec and Marquesas Islands (Figure 5). However, no significant migration rates were detected from the Atlantic Ocean to the Pacific, or reciprocally, a result that persisted when Round Island was removed from the analysis. Despite this, the results presented here provide evidence for gene flow and admixture between Atlantic and Pacific species outside the Indian Ocean, and therefore support the *widespread gene flow* hypothesis.

Although there was no evidence of ascertainment bias (Ellegren et al., 1995) in the species-specific markers between the different species sampled (Appendix A), it would have been advantageous to have a larger microsatellite marker set containing markers homologous with complete primer specificity to all of the five study species. This would have increased the power of the analyses to detect genetic structure between Herald and Phoenix petrels particularly, and may have enabled the detection of Phoenix petrel genotypes on Round Island. However, it may be that these two species are not well resolved, as no detailed phylogenetic studies have been conducted on Pacific Herald petrels and Phoenix petrels. Nevertheless, the 12 markers used in this study were sufficient to detect genetic structure between the different species sampled.

In this study, the aim was to distinguish between two potential models of gene flow involving the Round Island *Pterodroma* population using microsatellite genotyping and geolocation tracking data. The traditionally held model was the *secondary contact model*, with Pacific and Atlantic Ocean species only existing together and hybridising on Round Island in the Indian Ocean. In the contrasting scenario, the *widespread gene*

flow model, species from the Pacific and Atlantic Ocean species would be expected to be found coexisting and hybridising outside the Indian Ocean, as well as on Round Island. Geolocation tracking was used to investigate the dispersal potential of petrels from Round Island.

Historically speaking, the population of petrels on Round Island consists entirely of immigrants from outside the Indian Ocean, and it was clearly seen in the STRUCTURE analysis (Figure 17) that the Round Island population appeared to be more admixed (43.2%) than Atlantic and Pacific populations (Figure 4). This may relate to the Hubbs' principle, or "desperation hypothesis" (Hubbs, 1955), whereby hybrids are a result of a deficiency in conspecific mating options for rarer species in a population of related species (Randler, 2002, Randler, 2006, McCracken and Wilson, 2011). However, some petrels in the Atlantic Trindade population were classified as having either Kermadec-type or Herald/Phoenix-type hybrid genotypes (17.8% and 4.4% of the sample, respectively), and one individual was classified as a pure Kermadec-type migrant (Figure 4). Similarly, Atlantic (Trindade-type) hybrid genotypes were found in Pacific Kermadec petrel populations (Ducie Atoll 4%; Juan Fernández Islands 17.9%; Kermadec Islands 18.9; Rapa Iti 24.1%), Herald petrel populations (Ducie Atoll 7.1%; Marquesas Islands 13.0%; Oeno Island 4.8%) and Phoenix petrel populations (Christmas Island 6.6%; Marquesas Islands 3.4%; Phoenix Islands 6.3%; and the Pitcairn Islands 11.1%, Figure 4). This evidence of population mixing supports the findings of Brown et al. (2011), who found that one sampled Ducie Island Herald petrel possessed a Trindade-type mitochondrial cytochrome *b* haplotype, in addition to some Ducie Island Herald petrels sharing haplotypes with Kermadec petrels from the Kermadec Islands.

While the results of the STRUCTURE analysis support the *widespread gene flow model*, these findings are apparently contradictory to the lack of migration from the Indian Ocean to the Pacific or Atlantic Oceans, or directly between the Pacific and Atlantic Oceans found in the BAYESASS analysis. Estimates of per generation migration rate suggested that there was a high level of gene flow from the Trindade petrel population of the Atlantic into the Round Island population 18.3 ± 0.04%, and likewise, migration from the closest sampled Herald petrel population (Marquesas Islands, 1.4 ± 0.01%) and the closest sampled Kermadec petrel population (Kermadec Islands, 4.8 ± 0.01%) to Round Island (Figure 5). However, no reciprocal gene flow was observed.

There are two main reasons why BAYESASS may have been unable to detect migrants in this instance. Due to the difficulty of gaining samples from the remote

islands of the Pacific and Atlantic Oceans, the number of genotyped individuals from each of the island populations was very small, on average 26.7 (S.E. = ± 1.7), whereas the number of genotyped individuals from Round Island was much larger (N= 484, Table 1). Without including Round Island, the sample sizes for other populations are therefore unlikely to include enough potential migrants to be detectable at a per-generation rate if the migration rates are very low (Meirmans, 2014).

Alternatively, gene flow between contemporary blood sampled populations and museum skin sampled populations may have been underestimated using BAYESASS, as the model assumes that populations are separated by only a few generations, usually taken as fewer than five (Wilson and Rannala, 2003, Chiucchi and Gibbs, 2010, Faubet et al., 2007). Generation time is difficult to estimate, so for this study it was assumed that the generation time for the study species was similar to other *Pterodroma*, at around 15 years (BirdLife International, 2015, Welch, 2011, Garnett et al., 2011, Garnett and Crowley, 2000, Wiley et al., 2012). Assuming a 15 year generation time, individuals sampled from the museum collection (1920–1930) and the blood sampled individuals (2005–2012) were temporally separated by a maximum of six generations, more than the recommended one to three. It is therefore possible that the migration rates between Round Island and museum sample populations in the Pacific (Herald, Kermadec, Phoenix and Murphy's petrels) may be underestimated due to the difference in generation time between them. However, when F_{ST} was calculated between contemporary and historical Kermadec petrel samples from the Kermadec Islands, there was no significant difference in genetic variation between the two temporally separated groups, and it was assumed that this lack of difference would be the same for all populations. This result is expected given the long generation time (~15 years) of *Pterodroma* petrels and because the populations have not been disturbed by any dramatic population crashes, making it unlikely that genetic drift would have a strong effect on the populations over such a short time period. The collection of modern samples would be useful to further studies; but the islands where these petrels are found are very remote and infrequently visited by researchers.

Although the number of tracked petrels from Round Island was limited (N = 116) two individuals were tracked making trips outside the Indian Ocean (Figure 6). The two tracks show the petrels departing from Round Island in opposite directions, and coming close to other colonies in the Pacific and Atlantic Oceans. This demonstrates the incredible dispersal ability of seabirds and the potential connectivity of their isolated populations. It is interesting that these two petrels were tracked travelling counter to estimated migration directions. Most surprisingly, the petrel travelling to the Atlantic

Ocean from Round Island appeared more genotypically similar to Kermadec petrels of the Pacific Ocean than Trindade petrels (61.9% assignment to the Kermadec-type cluster in STRUCTURE analysis). Kermadec-type individuals such as this clearly can and do make the journey into distant ocean basins on rare occasions, and this may be an indication of how Kermadec genotypes are arriving at the Trindade Islands. The possibility of Kermadec petrels visiting and potentially breeding in the Atlantic Ocean has been contested in the past (Imber, 2004, Imber, 2005, Imber, 2008, Tove, 2005), but both the genotyping and tracking data presented here adds evidence to support their presence in the Atlantic.

Of course, the strong philopatry of Procellariform seabirds means that not all visits to other breeding colonies will result in a switching of breeding locations. Both petrels tracked outside the Indian Ocean subsequently returned to Round Island, although both were initially caught and ringed as adults on Round Island, so their natal colonies are unknown. However, ringing records provide evidence of colony switching between the Pacific and Indian Ocean. During routine seabird monitoring on Round Island in April 2006, a small pale-plumaged petrel was discovered with a young chick (Tatayah, 2010). The petrel was ringed with an Australian band, and was identified as originally being captured as a Herald petrel on Raine Island in 1984, where it bred with the same partner until 1987 (Figure 6; King and Reimer, 1991). This individual was subsequently recorded as present on Round Island with an egg in October 2008 and again in May 2012.

To date the only well-studied instance of introgression between species of *Pterodroma* petrel is from Round Island (Brown et al., 2011, Brown et al., 2010), although mitochondrial and phenotypic study of a single museum specimen collected during the Whitney South Seas Expedition east of the Antipodes Islands is posited as a hybrid between a White-headed petrel (*Pterodroma lessonii*) and Soft-plumaged petrel (*P. mollis*) (Tennyson et al., 2013). Indeed there are few published examples of two-way hybridisation between other Procellariform species, and these are based on small sample sizes or single individuals (Brown et al., 2015, Moore et al., 1997, Holdaway et al., 2001, Tennyson et al., 2013, McCarthy, 2006). Naturally occurring three-way (compound) hybrids are rarer still in birds, although anecdotally described in ducks (Harrison and Harrison, 1965) and hummingbirds (McCarthy, 2006). Avian three-way hybrids are more commonly reported in captive-bred birds such as pheasants, falcons, and cage birds (McCarthy, 2006). Here, not only are inter-species hybrids widespread between the populations of tropical *Pterodroma*, but possible three-way hybrids are occurring on Round Island (8.1%) and outside the Indian Ocean (Kermadec petrels:

Juan Fernández Islands 7.1%, Rapa Iti 6.9%; Herald petrels: Ducie Atoll 3.6%; Phoenix petrels: Pitcairn Islands 5.6%, Marquesas Islands 3.4%, Christmas Island 3.3%; Trindade petrels: 2.2%, Figure 4). This finding is therefore currently unique.

The results provide evidence of gene flow between three oceans in *Pterodroma* petrels, supporting the *widespread gene flow model* over the traditionally held *secondary contact model.* Within this complex of different species and island populations, Round Island is clearly an important zone of secondary contact between species originating in the Atlantic and Pacific Oceans. However, inter-ocean migrants and hybrids are not unique to Round Island. The wide-ranging behaviour of tropical *Pterodroma* may help them to disperse and colonise new or extirpated islands, and the potential to thrive in new environments bodes well for their future. This study highlights how little is known about gene flow and dispersal between populations of closely related, wide-ranging species. Consideration of migration and introgression with other species and colonies may be particularly relevant to the assessment of the conservation status and management of some seabirds. For example, the 'vulnerable' IUCN Red List status for the Trindade petrel (Birdlife International, 2016b) is based on its limited breeding range and therefore its susceptibility to stochastic events. The presence of this species in other locations, namely Round Island, should be taken into account for the Trindade petrel, and similar genetic and tracking studies concentrating in the Pacific may also provide valuable information for conservation efforts.

Chapter 3: An approach for recovering degraded geolocation data in animal tracking studies

3.1. Abstract

Light-level geolocation with archival tags is a widely used tracking method, and alongside its increased application to marine and terrestrial taxa, a range of geolocation software has been developed. However, as geolocation relies on the uninterrupted recording of sunrise and sunset events, shading of the geolocator during daylight hours leads to degradation of the archived light recordings, and not accounting for this can result in the generation of false locations. While some software can accommodate false shading events there is currently no applicable automated process available to clean false shading events for more advanced statistical geolocation analyses. This chapter presents a novel approach to eliminate interference caused by daytime shading noise in geolocation data, simplifying the geolocation process.

The `CleanLight` approach is an automated process that restores light data degraded by artificial shading events, identifies, and removes instances where the cleaning process has been unsuccessful. The extent to which false shading events can be corrected and at what level shading becomes irrecoverable is investigated. The approach is demonstrated on known light data with simulated levels of shading and on extensively shaded data taken from geolocators in a study of *Pterodroma* petrels at their breeding colony near Mauritius in the Indian Ocean.

Testing the `CleanLight` approach on simulated data revealed that it performed well at reconstructing a clean light data record for daytime shading frequencies up to 55%, which was well above the level of shading seen in the most degraded light files from petrels (17.6%, S.E. = ±0.7). When applied to real degraded data that were previously too disrupted to successfully generate locations using an advanced geolocation model, the light data were successfully recovered.

This new approach provides a standardised, objective approach for cleaning degraded geolocation data that can be applied to a wide range of study systems. The approach opens up advanced geolocation modelling to studies with degraded data by maximizing the information that can be gained from geolocator tracks. This is especially important for studies with a limited sample size or for tags fitted to species that exhibit high levels of light interference.

3.2. Introduction

Light-based geolocation is a method of estimating the location of an animal using an archival sensor that records time-stamped ambient light levels (Wilson et al., 1992), allowing the subsequent calculation of global positions by identifying times where light intensity changes due to sunrise and sunset events (Winship et al., 2012, Ekstrom, 2004). The sensors, known as Global Location Sensors (GLS) or more commonly 'geolocators', have been widely used to study the home ranges, migration routes and foraging hotspots of a diverse range of terrestrial and marine species, including sharks (Lam et al., 2010), tuna (Schaefer et al., 2011), seals (Sumner et al., 2009), seabirds (Bost et al., 2009, Catry et al., 2011, Guilford et al., 2011, Le Corre et al., 2012, Rayner et al., 2012, to name but a few) and even small passerines (Bairlein et al., 2012, Seavy et al., 2012, Renfrew et al., 2013). Geolocators are particularly useful to track large samples of birds at a broad spatial scale (over 1000km range), due to their light weight, relatively low-cost and long battery life.

With the growing popularity of geolocators, the options for calculating locations from raw light data have increased, and a number of possibilities are available to increase the accuracy of location estimates. The most widespread methods are based on the *threshold method*, where latitude is estimated based on day length, and longitude on the timing of local midday or midnight (Hill and Braun, 2001, Fox and Phillips, 2010, Wilson et al., 1992, Hill, 1994). More recent statistical models are often based on the *template-fit method*, and improve the accuracy of location estimates (Bograd et al., 2010, Rakhimberdiev et al., 2015, Ekstrom, 2004). Newer template-fit based statistical geolocation models include the ability to calculate the uncertainty associated with location estimates, allowing biological inferences to be more readily distinguished from observational noise in tracking data (Bograd et al., 2010, Winship et al., 2012). Perhaps the most important advantage of the modelling approach is its flexibility. The accuracy of location estimates can be improved by factoring in constraining filters such as maximum speed and habitat (Sumner et al., 2009) and by refining estimates using supporting data such as: chemical readings (Lam et al., 2010), depth (Nielsen et al., 2006, Sumner et al., 2009) and sea surface temperature (SST), also recorded alongside light data. Refining location estimates by filters and constraints in this way is particularly advantageous to geolocation studies, as geolocators have a lower spatial resolution than other tags, such as satellite transmitters (Phillips et al., 2004).

However, most geolocation methods do not have a specific filter to address the problem of interrupted light data. Noise in the light data may consist of artificial light

recordings during the night, but more usually involves recordings of darkness during a daylight period, which occurs when the light sensor on the geolocator experiences shading. These daytime shading events may be caused by vegetation (Lisovski et al., 2012, Fudickar et al., 2012) or shading by the host animal itself (Ramírez et al., 2013). Shading by the host is a common source of noise in geolocation studies, particularly when geolocators are leg-mounted, as is conventional with seabirds (Cleeland et al., 2014, Gutowsky et al., 2014, Le Corre et al., 2012, Ramírez et al., 2013, Reid et al., 2013). The software `BAStrak` (British Antarctic Survey (BAS), Cambridge, UK) that accompanies one of the most widely used makes of geolocators (formerly BAS, now Biotrack, Wareham, UK) is still a popular method of deriving locations from light recordings. While `BAStrak` lacks features such as filters and constraints available in other geolocation analyses, it includes a 'minimum dark period' filter that removes false sunrise and sunset transitions by identifying areas of shading that fall under a user-specified duration (Fox and Phillips, 2010). Without an equivalent method for removing erroneous transitions from the data prior to analysis in more advanced geolocation analyses, such as `tripEstimation` (Sumner and Wotherspoon, 2012), `Geolight` (Lisovski and Hahn, 2012) and `FlightR` (Rakhimberdiev et al., 2015), degraded light data can cause a range of problems in the estimation of locations via geolocation.

Discarding data from days where disruptive shading occurs, particularly when it occurs near or during a transition time, is a common practice in studies using the `BAStrak` geolocation method (Fox and Phillips, 2010) and degraded data may also be removed prior to processing with other geolocation methods (Seavy et al., 2012, Lisovski and Hahn, 2012, Rakhimberdiev et al., 2015), for example using the online interface TAGS (Totally Awesome Geolocator Service; http://tags.animalmigration.org). In these cases, the user must judge all transitions between light and dark to decide whether they are useable for further analysis or falsely generated and discard degraded data accordingly. Understandably this process is subjective, extremely time-consuming and unlikely to be repeatable. In addition, depending on the ecology of the organism being studied and hence the degree of shading present in the light data, discarding data in this manner may greatly reduce the amount of information available from geolocation.

This chapter presents an automated approach for recovering shaded geolocation light data based on 'cleaning' daytime shading noise and removing days where shading is too severe to recover. The approach aims to maximise the amount of useable data available to geolocation studies working with degraded light levels. A standardised framework for cleaning geolocation data that minimises observer bias and thereby increases the reproducibility of results is proposed. Application of the approach is

demonstrated both on a clean dataset with simulated shading and on naturally degraded data retrieved from geolocators deployed on a population of gadfly petrels (*Pterodroma* spp.). The limitations of the approach are identified and discussed, particularly where shading is too extensive to recover data, and further suggestions on how best to address this are provided.

3.3. Methods

The `CleanLight` data cleaning approach

All the scripts for the data cleaning approach are available for users at https://github.com/Zoological-Society-of-London/clean_light.git and in Appendix B. CleanLight can also be used as a Shiny web application: https://robfreeman.shinyapps.io/cleanlight_shiny. The process of cleaning degraded light data requires two main scripts collected together and run from a single script, called the `CleanLight_link_script`.

1. `cleanlight`

The `clean_light` function was originally created to remove noise in Wedge-tailed shearwater (*Ardenna pacifica*) geolocation data caused by feather shading, but was modified for this study system. The function retains transitions between night and day in the light file, while unusual light level measurements, in the context of the data in the surrounding window are replaced with either the maximum light measurement, 64 or a darkness measurement, zero (Fox and Phillips, 2010). It does this by scanning forwards and backwards along the light data using a window of a user-defined range (number of points, '`npts`') to identify areas where recorded light levels are not consistent between adjacent time steps, i.e. jumping between recordings of the maximum light intensity and short periods of shading.

- Positive and negative changes in light measurements are calculated.
- A vector is populated by maximum and minimum light measurements based on the number of maximum light measurements, number of positive changes and number of negative changes in measurement within the '`npts`' window.
- Light periods shorter than the '`npts`' window are examined for jumping light levels, and these are replaced with maximum or minimum light measurements.
- The script outputs a dataframe of the 'cleaned' data.

2. remove_suspect_days

When a shading event totally masks a sunrise or sunset the `clean_light` function is unable to locate the true transition time between day and night, and vice versa. This can result in a shortening of the overall day length for that day. The `remove_suspect_days` script removes days where the `clean_light` function fails to reconstruct the shaded light data accurately.

- Day lengths are calculated from the light data by calculating differences in successive sunrises identified using the geolocation package `Geolight` (Lisovski and Hahn, 2012).
- Days that are greatly shorter than the previous day are identified and removed. For the petrel data, mean day length plus one standard error was used as the threshold argument to identify suspect days, although if the user expects large or small differences in day length due to the ecology of their study organism, this can be changed in the `remove_suspect_days` script accordingly.
- The previous step is repeated iteratively, removing days that violate the threshold up to a maximum likely change, set using the `max_day_diff` argument. This reflects an approximate maximum likely change in day length possible given the maximum speed of travel of the study organism.
- The script outputs a light file with the shortened days removed.

Testing

Shading simulation

In all geolocation studies geolocators must be calibrated, and frequently unattached geolocators are used for this purpose (Fox and Phillips, 2010). To test the data cleaning approach, I used uninterrupted light data from a Mk15 British Antarctic Survey (Cambridge, UK) calibration geolocator left exposed on Round Island (19˚85’ S, 57˚78’ E), off the coast of Mauritius, Indian Ocean. These geolocators sample light each minute and log a maximum light measurement at 10 minute intervals (Fox and Phillips, 2010). During the night, or if covered during the day, geolocators record a light measurement of zero. During the day, if the tag is not covered or obstructed, it will record a maximum light measurement of 64. To generate an example dataset with

which to test the data cleaning approach, artificial shading was applied to the maximum light measurements made by the static calibration geolocator. Using the `runif` function in R to generate independent uniform random variables between 0 and 1, maximum light measurements were randomly replaced with a value of zero, at frequencies from 0% shaded to 95% shaded, in increments of 5%. The shading treatment was iterated to generate 100 replicates at each increment. Artificially shaded files were then processed using the data cleaning scripts as previously outlined to produce cleaned light files.

Coordinates were created from the cleaned light files using the geolocation R package `Geolight` (Lisovski and Hahn, 2012), and a root mean square error difference was calculated between the original uninterrupted light file, and each of the cleaned files. Additionally, distances between the mean coordinate of each cleaned file and the mean coordinate from the original file were generated.

Effect on the estimation of distribution area

Light and sea surface temperature data were recorded by leg-mounted geolocators on a hybridising population of *Pterodroma* petrels (*P. arminjoniana, P. neglecta* and *P. heraldica*) at their breeding islet, Round Island (Tatayah, 2010, Brown et al., 2010, Brown et al., 2011). Between November 2009 and February 2011, 220 Mk15 BAS geolocators were deployed on adult petrels. Each tag was mounted on a flexible ring made from 1mm or 0.75mm thick industrial grade PVC (Salbex), and was subsequently fitted on the petrel's tarsus. Of the 220 geolocators deployed between 2009 and 2011, 120 were recovered with useable data. The time period recorded by petrel-mounted geolocators often included both migratory data and data collected whilst petrels were based at Round Island, potentially during breeding attempts. Of the 120 recovered geolocators, 95 contained at least 60 consecutive days of data collected at the breeding colony.

Light files from 5 of these petrels were artificially shaded at a 5% and 35% frequency in addition to the naturally occurring shading caused by the behaviour of the petrels. The original light files, plus the artificially shaded light files were cleaned using the `CleanLight` approach. Locations were then generated from the original light files, the cleaned original light files, and from both of the cleaned, artificially shaded datasets. The geolocation model used was based on Thiebot & Pinaud's (2010) implementation of the '`tripEstimation`' package developed by Sumner and Wotherspoon (2009) in the programming environment R (Sumner and Wotherspoon, 2012, R Development

Core Team, 2013). Isopleth contours incorporating 95% (peripheral range) and 50% (core range) (Ramírez et al., 2013, Paiva et al., 2010b) of locations from colony-based birds were generated for the 5 petrels using the original data, cleaned original data, cleaned 5% shaded data and cleaned 35% shaded data, using the Spatial Ecology software GME (Beyer, 2012b).

Application

For the 120 recovered petrel-mounted geolocators, Thiebot & Pinaud's (2010) implementation of `tripEstimation` reliably produced location estimates during the petrels' non-breeding migratory period during which petrels were entirely at sea, but when petrels were associated with the breeding islet, there was considerable noise (i.e. false shading events) caused by the petrels sitting on top of the geolocators whilst at their nest sites. Preliminary examination of a sub-sample of 30 from the 95 light data recordings associated with petrel presence at Round Island revealed a variety of shading interruptions. These ranged from short dips in daytime light recordings indicating brief visits to the island, to sustained periods (days) of interruption in daytime light recordings, possibly associated with incubation. In the most extreme cases, where a high degree of shading was present in the light file over multiple days, the `tripEstimation` model completely failed to run on the data, resulting in no locations generated for 26.6% (N=8) of the light files from the sub-set. This is a very large reduction in the sample size and if scaled up to the full sample size of 95 colony-based individuals, it equates to a loss of approximately 25 tracks. To address this problem, the 8 degraded geolocation datasets were processed using the `CleanLight` approach with a `npts` value of 36 data points and a `max_day_diff` value of 100 minutes, prior to analysis in the `tripEstimation` model.

3.4. Results

The effect of the CleanLight script on location estimation

Shading simulation

The `CleanLight` approach was used to process a total of 2000 simulated light datasets: 100 replicates of each 5% increment of daytime shading, from 0% to 95%. Figure 7 shows how successfully the cleaning approach reconstructs the artificially shaded light files. As the percentage of daytime shading increases, the root mean

square error difference between the coordinate of the corrected file and the coordinate of the original file also increases (Figure 7A). The difference is also demonstrated in terms of distance in kilometres (Figure 7B); the distance of the coordinates from the cleaned file from those generated from the original increases as the shading applied to the light recording increases. However, the distance error does not exceed the typical error value for the geolocators themselves, 186 ±114 km (Phillips et al., 2004), until the day time shading increases beyond 55% of the total day time light recordings.

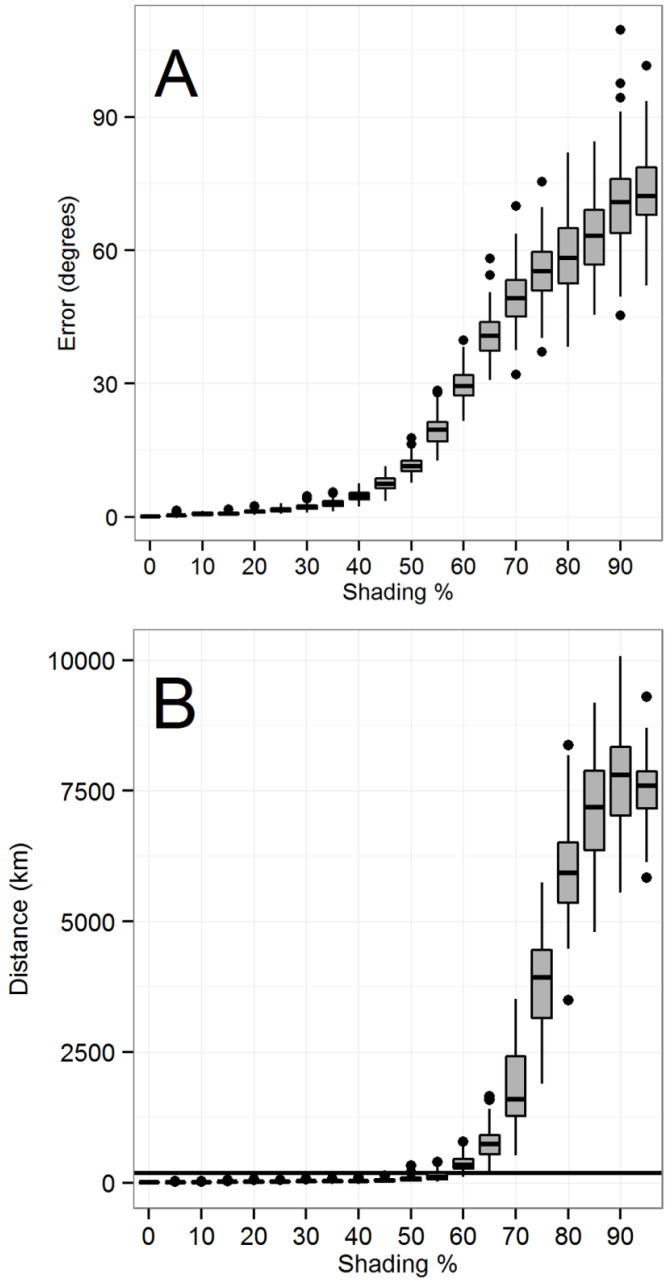

Figure 7: Increasing the percentage of day-time shading occurring in the simulated light files increases the root mean square error between the original light file coordinates and the corrected file (A) and increases the mean distance of the corrected file coordinates from the coordinates of the original file (B). The error distance for geolocators (186km, Phillips et al., 2004) is represented by the black line (B).

Figure 8 illustrates how calculated locations are affected after recovery with the `CleanLight` process at increasing proportions of daytime shading of the original file. At lower levels of daytime shading, for example 5% and 35%, locations generated from the recovered light data are close to the locations generated from the original static geolocator light data. At 65% daytime shading, recovered location estimates are further from the original location, and at 95% shading, location estimates are widely scattered west of the true location, as expected with shading retarding sunrise and advancing sunsets.

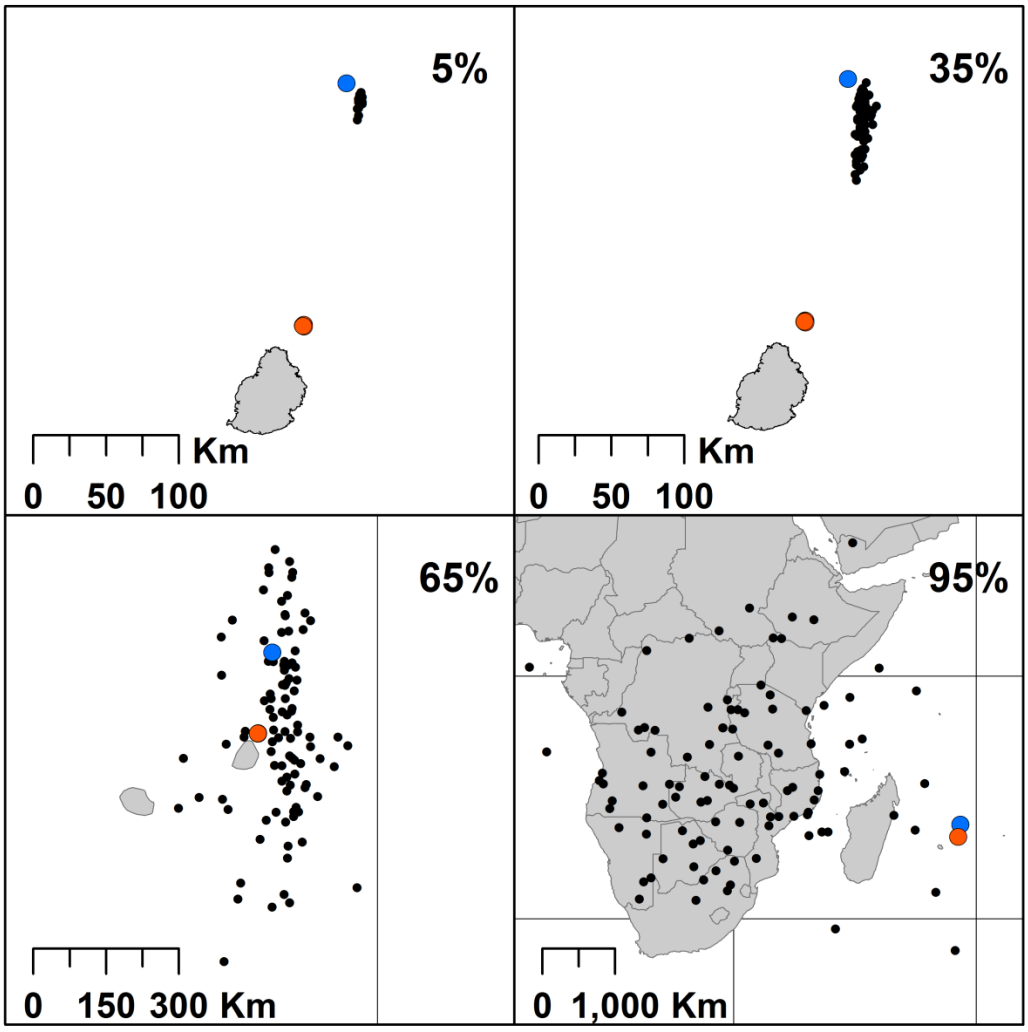

Figure 8: Maps showing the position of the mean locations (solid black circles) derived from each replicate of the cleaned light files for four different degrees of shading; 5%, 35%, 65% and 95%. The position of Round Island is indicated by the red circle, and the mean location derived from the calibration geolocator is indicated by the blue circle.

Effect on distribution isopleths

The effect of the `CleanLight` approach on location estimates made from real petrel geolocator data was tested on 5 individuals with data that ran successfully through Thiebot & Pinaud's (2010) implementation of `tripEstimation` prior to any cleaning. The breeding season locations of these 5 petrels were generated using the original light data from the geolocators, the original data processed with the `CleanLight` approach, and cleaned data that had previously had the daytime shading artificially increased at 5% and 35% frequencies. The isopleths generated from these locations can be seen in Figure 9. If the `CleanLight` method was causing systematic errors in the generation of location estimates from light recordings in the model, the resulting cleaned distributions might be expected to look very different to the original distribution (Figure 9, top left). However, both the 95% range distributions and the 50% core distributions of all the locations generated from cleaned data are very similar in size and shape to the original, even when the frequency of shading applied to the light files is high, at 35%.

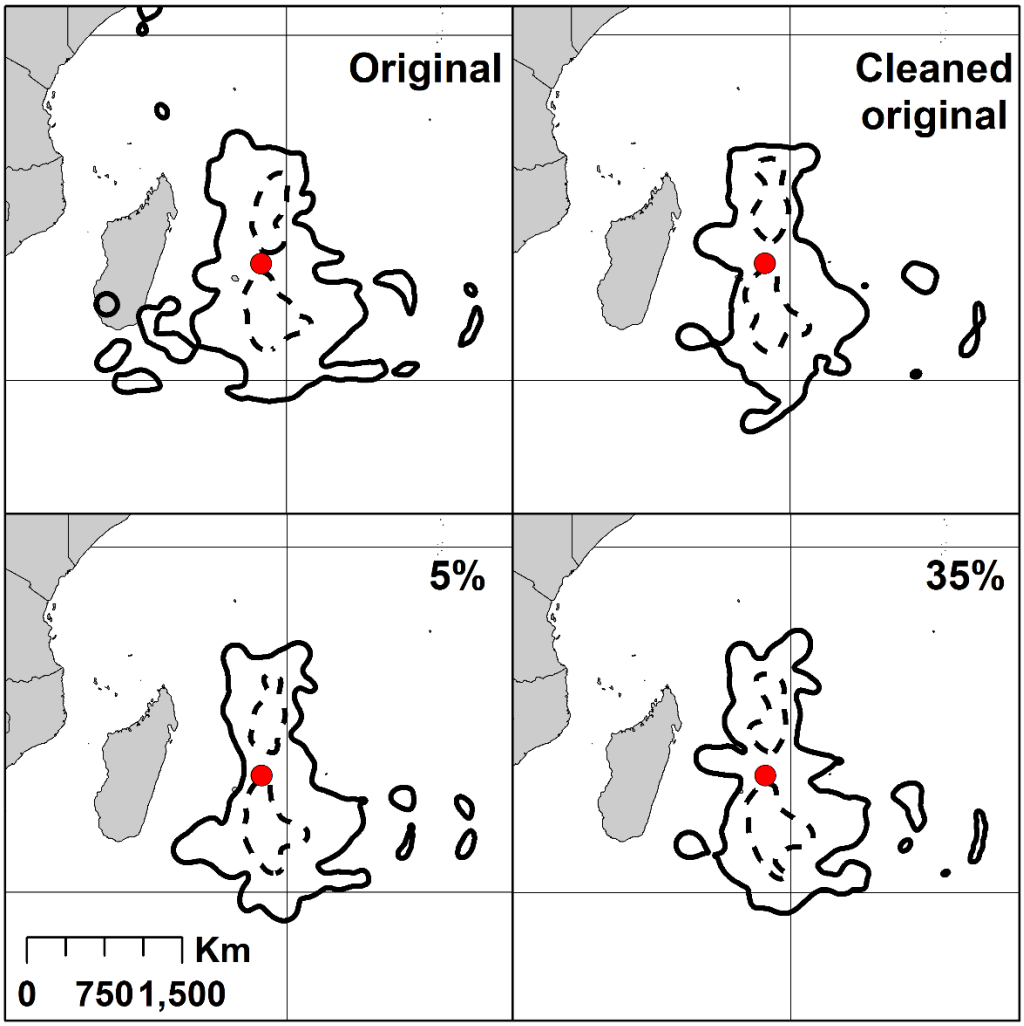

Figure 9: 95% (solid line) and 50% (dashed line) isopleths applied to 5 petrel light files that initially ran through the tripEstimation without alteration. The top left map (Original) represents the isopleths of the original light files without any correction. The map in the top right shows the same isopleths after the CleanLight process has been applied to the original data. The bottom two maps show the isopleths generated after the CleanLight method is applied to the 5 petrel light files corrupted with an additional 5% (bottom left) and 35% (bottom right) shading frequency. The location of Round Island is indicated by the red circle.

Recovery of degraded breeding season geolocation data

Out of a subsample of 30 light files, 26.6% failed to run through `tripEstimation`. However, once these files were cleaned using the `CleanLight` approach, all degraded tracks could successfully be processed with the model, alongside their sea surface temperature data, to increase the accuracy of the location estimates.

Previous to recovery, the 8 light files that failed to run through the `tripEstimation` model had an average daytime shading percentage of 17.6% (S.E. = ±0.7), compared to the average day length from the static geolocator light file (74 maximum light recordings). This percentage is much lower than the point at which the `CleanLight`

approach begins to fail at reconstructing randomly shaded light files (55%). After processing with the `CleanLight` approach, the daytime shading percentage fell to 1.3% (S.E. = ±0.3), and an average of 30 (S.E. = ±6) irrecoverably shaded days were removed from each of the files, out of an original average tracking period of 134 days (S.E. = ± 13) for these 8 petrels. Figure 10 shows the number of maximum (i.e. unshaded) light measurements recorded per day in the uninterrupted light file from the static geolocator (Original), compared to the number recorded per day in the heavily shaded (Shaded) and recovered light files (Corrected).

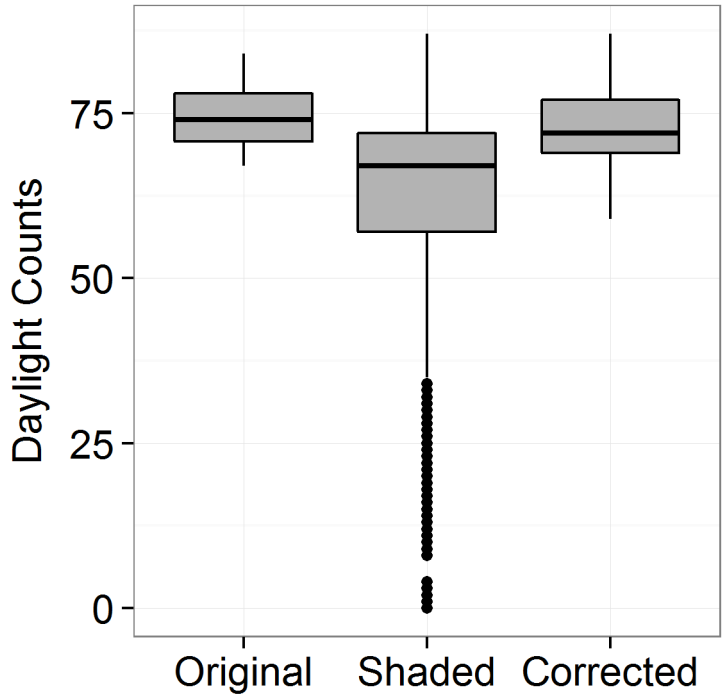

Figure 10: The number of maximum light readings (of 64) per day in the static geolocator (Original), petrel light files that initially failed to run through tripEstimation (Shaded), and the same files after cleaning (Corrected).

3.5. Discussion

The `CleanLight` data cleaning approach described here allows the user to systematically clean degraded light data, which is highly desirable as new geolocation analyses provide many advantages over more simplistic location estimation techniques, such as location filters and constraints.

The extent to which the approach can recover shaded data was explored using a dataset with simulated shading. It was found that random occurrences of shading in a daylight period could be reasonably reconstructed to reflect the original file up to a level

of 55% of daytime shading (Figure 7) before the locations calculated from the reconstructed file differed from the locations generated from the original by a distance of more than the known error distance of geolocation tags, 186 ±114 km (Phillips et al., 2004). This greatly exceeds the average shading recorded in light data that could not be used in Thiebot & Pinaud's (2010) implementation of `tripEstimation` in this study (17.6%). It is recommended that `CleanLight` is best applied to light files where the extent of day time shading can be calculated, for example by comparing to equivalent light recordings from an unshaded tag. However, it is acknowledged that shading may not always occur in a known area. It is not recommended for use on files where the daytime shading is evenly distributed throughout the daylight period and regularly exceeds 55% shading, as locations generated from the recovered light data are likely to be unrealistic (Figure 8). The temporal distribution of shading events throughout the daylight period influences the cleaning process; if shading is concentrated near to a transition time, it will be removed from the dataset during the `remove_suspect_days` step, unless the shading is shorter than the allowed variance specified by the user in the `max_day_diff` value. In this case the locations estimated from the light data may be biased westwards, and should be treated with caution. It should be noted that artificial shading applied to light data randomly at different levels of frequency is unlikely to mimic shading caused by an organism's behaviour or habitat preferences, which may be autocorrelated between days. In addition, the method of using a scanning window to search for jumping light levels is likely to perform better at removing random shading noise from a sequence than autocorrelated bouts of shading, for example, where consecutive days are reduced by the same degree. Consistent daytime shading may occur in species that regularly return to burrows or cavities, shelter in dense vegetation or tuck the sensor under fur or feathers. This shading pattern around twilights can cause large errors in the calculation of true sunrise and sunset times, and users with this type of data should proceed with caution. Visual inspection of light data is always an important step in the geolocation process.

Despite these limitations, the `CleanLight` approach appeared to perform well in reconstructing petrel geolocation data with real shading events. This was demonstrated using 5 light files, comparing the distribution of locations generated from the original to those generated from corrected light files at three different levels of shading (Figure 9). Isopleth lines representing 95% and 50% of the total locations generated in each dataset demonstrate how little effect the `CleanLight` approach has on estimated location distributions, even when the applied shading frequency greatly exceeds that seen in real data. Although some small differences in the shape and size of the

distributions are evident, this is unlikely have a strong bearing on conclusions made about the range or core areas of usage for wide-ranging species, which is the common goal of geolocation studies (Phillips et al., 2004).

The mean percentage daytime shading in the 8 degraded light files collected from petrels fell well below the limit of 55%, at 17.6% (S.E. = ±0.7). This degree of shading caused these files to fail to run through the `tripEstimation` model, but after cleaning, all files were processed successfully. After the application of the `CleanLight` approach, the number of maximum light measurements per day in the degraded files, a proxy for day length, was restored to that of the uninterrupted light recordings made by the calibration geolocator on Round Island (Figure 10). Scaling this recovery of previously unusable light files up to the full sample size of 95 geolocator light files with a mean duration of colony attendance of 119 days (S.E.= ±4), equates to a potential recovery of 6014 position estimates (S.E. = ±202, two estimates per day) out of a possible 22610 (S.E. = ± 760), that would otherwise have been lost. This compares favourably to the number of position estimates removed per light file during the `CleanLight` approach. If 26.6% of the full sample size of 95 light files were heavily shaded and recovered using the `CleanLight` approach, losing an average of 30 days per file, this totals a loss of approximately 1540 position estimates, rather than 6050 with no recovery.

It is important to note that the `CleanLight` approach is not only useful to restore previously unusable light files, but also removes daytime shading from files that can be successfully processed with geolocation models without the removal of these minor shading events. Low levels of shading present in light files may be accidentally included and processed using the geolocation models without causing error messages to arise, but the effect they may have on the location estimates is uncertain and would depend on the geolocation method and extent and timing of shading. Therefore whilst geolocation models currently require the user to evaluate and remove shading from each light file before analysis, the `CleanLight` approach's automation makes it both more time-effective and objective than the manual removal of shading from a dataset.

Although the aim of maximising the objectivity and repeatability of this approach for reconstructing corrupted light data, a number of decisions must be made by the investigator prior to the data cleaning process. These decisions rely on the user being familiar with their data and the ecology of the system they are studying, and therefore visual inspection of the recorded light data is still an essential step in the process. Firstly, a suitable scanning window width (`npts`, used in the `clean_light` function)

to scan the data for jumping light levels must be chosen. This decision should be made taking into consideration the recording frequency of the geolocator, biology of the study system and the level of disruption seen in the data, but also involves some trial and error to identify a number that restores the data without obscuring transition times. This is where manipulation of a clean baseline dataset can be helpful for testing different window widths. Since each data point included in the scanning window represents light recordings over a set interval, the selected value of `npts` should include a time frame that is likely to include more data points that are unaffected by shading than those that are. If the window is too narrow, the `clean_light` function will reduce the frequency of shading periods in the data, but may not eliminate them completely. Too wide a width will reduce the accuracy of restoring true transition times. For the petrel data, a scanning window of 36 data points worked well, so this is recommended as a starting point.

Secondly, the observer must judge the level of acceptable variation (`max_day_diff`) to be left in the data during the second function, `remove_suspect_days`. Mean day length difference and standard deviation are used in this case, but it may be more appropriate for other studies to set a higher or lower threshold for identifying outliers. This could depend on the travel speed of the species in question; how much variation in day length is likely given the amount of distance it can travel in a set time. For example, large gadfly petrels, such as those studied in this system, travel at an average speed of around 45.7 (±12.63) $km \cdot h^{-1}$ (Spear and Ainley, 1997), whereas smaller species in the Order Procellariiformes, for example *Oceanodroma* storm petrels have a much lower average speed of 26.63$km \cdot h^{-1}$ (±7.63$km \cdot h^{-1}$) (Spear and Ainley, 1997). Additionally, a species may plausibly reach speeds that far exceed its average speed: whilst Cleeland et al. (2014) found that the mean flight speed of Short-tailed shearwaters (*Puffinus tenuirostris*) was 17.9±0.3$km \cdot h^{-1}$, they measured a maximum speed of 76.6 $km \cdot h^{-1}$. This reasonable variation needs to be taken into account when setting both the `max_day_diff` for `remove_suspect_days`, and when parameterising the movement model in more advanced geolocation analyses, as failure to do so will result in position estimates lagging behind the true movement of the tagged host. While the standard deviation takes into account the overall variation present in a dataset, it may also be worth considering the expected genuine variation in day length caused by the movement of the host animal. This could mask the effects of false correction by the `clean_light` function and therefore it may be appropriate to adjust the threshold for error identification accordingly. It is recommended that the user be liberal with the amount of variation allowed by the `remove_suspect_days`

function, as advanced geolocation models such as `tripEstimation` include filters to constrain unlikely location estimates. For example, if shading totally obscures a genuine sunrise or sunset transition, and this is subsequently not removed by the `remove_suspect_days` function, geolocation model filters such as speed restrictions or sea surface temperature matching may either remove the point from the analysis because it violates the model's constraints, or reposition it at a plausible location given these constraints (Thiebot and Pinaud, 2010). Errors may arise if a false transition causes a difference too small for any of the data filters to detect. If this is the case, a false transition can affect not only the location estimate at the time of the error, but also the preceding and subsequent location estimates. However, geolocation is not a precise method of acquiring locations and is not generally used to examine fine-scale movement patterns, so small deviations should not affect the overall validity of conclusions made about broad scale distribution patterns. The main aim of the `CleanLight` approach is not to identify and combat errors in the estimated track itself, but to clean interference in light data and identify times where the correction process has mistakenly altered day length.

Conclusion

In the past, studies focusing on geolocation data from species that frequently shade their geolocators have used manual methods to reduce noise in their data. The `BAStrak` method, along with others such as the `Geolight` (Lisovski and Hahn, 2012, Lisovski et al., 2012) and `FLightR` (Rakhimberdiev et al., 2015) packages in R, require the observer to make subjective judgements of the reliability of every transition prior to analysis, and those judged to have a low confidence are removed (Fox and Phillips, 2010). Consequently large amounts of data are lost, which may be of particular concern in studies with small sample sizes. Not only does treating degraded light data in this way reduce the amount of useable data available to a study, it also adds a very time-costly step to the geolocation process, and is prone to observer bias.

The `CleanLight` approach to recovering degraded light data detailed here contributes to the standardisation of geolocation analysis, using automated scripts that save time whilst minimising observer bias, thus increasing the repeatability of results. For large studies, the time-saving automation may be particularly beneficial, although careful visual inspection is still an essential step towards preparing light data for geolocation analysis. Correcting and conserving corrupted geolocation data, rather than discarding it, will be of benefit to studies with small sample sizes or on species that frequently

shade their geolocators, and will better enable the identification of important broad-scale movement patterns in these systems.

Chapter 4: The importance of quantifying intra-population variation in the at-sea distribution of colony-based seabirds when identifying marine hotspots

4.1. Abstract

Seabird distribution studies are useful to identify hotspots for marine protection, but intra-population variation in distribution is often neglected. Tropical seabird populations are currently under-represented in the literature and may be particularly prone to intra-population variation due to the oligotrophic and unpredictable nature of tropical oceans. Here, substantial intra-population variability is demonstrated in the distribution of Round Island (*Pterodroma*) petrels breeding at a single colony in the Indian Ocean, using a novel Bayesian Mixtures Analysis.

While population-level density estimates broadly revealed the distribution of petrels around the colony, variation was found within comparable periods; 14 distinct distribution patterns were found between 85 individual petrels during two months following the non-breeding migration, and 13 patterns were found between 71 individuals prior to leaving on migration. Considering this intra-population variation in the identification of important areas increased the core distribution estimate of this population by 47.8 - 79.6%, depending on the time period considered. Overlooking intra-population variation may therefore significantly underestimate the core distribution of seabird populations.

This study is the first of its kind to look at individual variation in the colony-based, at-sea distribution of a closely-related, mixed species population of tropical seabirds, demonstrating that even during a period of the annual cycle thought to limit distribution, petrels do not all behave in the same way. Representing variation in the distribution of seabirds is vital when identifying marine hotspots for protection, as intra-population behavioural plasticity is key to maintaining biodiversity and sustaining populations in the face of future change.

4.2. Introduction

Pelagic seabirds may be the most wide-ranging taxa in the world, but despite their mobility they are also one of the most threatened groups of birds globally (Croxall et al., 2012). Marine ecosystems are suffering under ever-increasing human pressures (Halpern et al., 2008) and as such seabirds face a number of threats at sea, such as pollution, fisheries and climate change (Croxall et al., 2012, Le Corre et al., 2012), both in their breeding ranges and during migrations away from the colony.

Distribution data from biotelemetry studies is of vital importance to conservation planning, as knowledge of the distribution of a species can identify areas where species may be at risk from human threats (Suryan et al., 2007, Birdlife International, 2004). Identifying and protecting areas that breeding seabirds rely on whilst colony-based may be critical to the conservation management of some species. This is because breeding seabirds are particularly restricted in the foraging areas they can visit by the need to return to incubate an egg or feed a chick (Weimerskirch, 2007), making foraging areas around the colony essential to the breeding success of the population (Thaxter et al., 2012, Maxwell and Morgan, 2013).

Many studies identify ecologically important areas for seabirds using distribution data from tracking studies. However, not all individuals in a population may spatially behave in the same way. To date distribution studies have considered variation mostly between colonies of the same species (Frederiksen et al., 2012, Rayner et al., 2008, Weimerskirch et al., 2015, Catry et al., 2011) or between species breeding at the same island/location (Robertson et al., 2014, Thiers et al., 2014, Navarro et al., 2015). Few studies take into account potential intra-population differences of a seabird species in the foraging areas they use during their breeding period, a crucial stage of their life-cycle (although see Waggitt et al., 2014, Ramírez et al., 2015, Navarro et al., 2009d). This may be because until recently tracking devices were expensive, prohibiting the large sample sizes needed to explore intra-population variation in distribution patterns from a single species at a single colony. We have also lacked the analytical techniques that would allow objective testing for individual differences in distribution without imposing an *a priori* structuring on individuals in the study. Additionally, many studies focus on temperate or polar species where there is a clearly defined breeding season and prey availability is predictable spatially, seasonally and inter-annually, making seabird populations more likely to be consistent in the areas they target. However, little is known about the diversity in the distribution patterns of tropical seabirds whilst they are associated with their breeding islet. For tropical species particularly, where prey

availability is more ephemeral and unpredictable than in temperate and polar biomes (Monticelli et al., 2007, Jaquemet et al., 2007, Hennicke and Weimerskirch, 2014, Weimerskirch, 2007), intra-population plasticity in distribution may be quite common place and potentially advantageous.

It has been shown that individual variation in space-use can have significant effects on the apparent distribution of a population, depending on the number and selection of individuals sampled (Gutowsky et al., 2015). Incidences of intra-population variation should therefore be taken into account when designating areas for protection (Lascelles et al., 2012), both for marine and terrestrial systems. This is particularly significant when considering that it is important to maintain diversity in populations (Reed and Frankham, 2003, Wolf and Weissing, 2012), particularly threatened ones, as many seabird populations are. By not taking into account intra-population variation in at-sea distributions we may be neglecting to protect diversity in those populations. The western Indian Ocean is a hotspot for marine biodiversity, including cetaceans, turtles, tuna and billfish, and supports 31 species of seabirds (Le Corre et al., 2012). Despite this, less than 1% of the Indian Ocean is included within a Marine Protected Area (Le Corre et al., 2012), and therefore identifying ecologically valuable areas is a priority.

This study focuses on the *Pterodroma* spp. colony at Round Island, off the coast of Mauritius in the Indian Ocean. Nothing is currently known about the colony-based distribution of Round Island petrels and given the lack of pelagic protected areas in the Indian Ocean, Round Island petrels may be exposed to threats at sea during their time at the colony. This study therefore aims to identify marine areas of key importance to Round Island petrels, and investigate possible intra-population variation in distribution around the colony. The study quantifies variability at across the entire colony-based period, within comparable life-cycle periods and within individuals at different periods of their time at the colony. Round Island petrels are expected to show high levels of intra-population variation in their distributions across both the entire colony-based period and within comparable stages of their colony-based period due to their asynchronous breeding cycle and the population's compound-hybrid status (Brown et al., 2010, Brown et al., 2011).

4.3. Methods

Data collection

Data collection for this study took place on Round Island (19.85º South, 57.78º East, Figure 20), off the coast of Mauritius in the western Indian Ocean. Round Island petrels can be found surface-nesting at the colony all year round, although peak egg laying occurs between August and October (Tatayah, 2010). The population consists of a hybrid mix of three species of *Pterodroma* (gadfly) petrel, the Trindade petrel (*P. arminjoniana*), Kermadec petrel (*P. neglecta*) and Herald petrel (*P. heraldica*) (Brown et al., 2010, Brown et al., 2011, Chapter 2).

Between November and February of 2009-2011, 135 and 85 Mk 15 geolocators (British Antarctic Survey) were deployed on adult petrels respectively (for details of capture of petrels and attachment method, see Nicoll et al. (2016) and Appendix C). The two consecutive deployments (2009-2010 and 2010-2011) of geolocators were mounted on different coloured Salbex rings to avoid the early recapture of more recently deployed geolocators during the second deployment. Petrels with geolocators were recaptured opportunistically during seabird monitoring from the October following the deployment period, after which petrels were presumed to be returning from a migration. Of the 220 geolocators deployed between November 2009 and February 2011, 103 (76%) and 63 (74%) were recovered from the 2009-2010 and 2010-2011 deployments respectively. All recovered geolocators were calibrated at a known location before and after deployment for three to five days, and of the 166 recovered geolocators 119 contained useable light, sea surface temperature (SST) and immersion data, which were downloaded and decompressed using the British Antarctic Survey software `BAStrak` (Fox and Phillips, 2010).

Data processing

The petrels' return and departure dates to and from Round Island were identified visually using immersion data (a marked dip in daily immersion corresponding to a return to land) and light data (interrupted daily light recordings indicating the petrel resting on the geolocator). From the viable geolocation data, only those with at least one period of 60 days or more spent at Round Island were included in the further analysis. This was to identify petrels staying at Round Island, rather than passing through. Since 60 days is approximately the time it takes for a Round Island petrel egg to hatch from its laying date (Tatayah, 2010), petrels present at the island for this

amount of time or more could potentially be involved in a breeding attempt. Of the 119 viable geolocators, 95 contained at least one period of 60 days at Round Island, before or after a migratory period, and some had both. Included in these, 23 colony-based tracks were captured between two migratory periods, therefore representing the complete distribution for a petrel's colony period.

Due to their asynchronous breeding cycle and the indeterminate nature of their nests, it is prohibitively difficult to confirm the exact breeding status of individual petrels at Round Island. Therefore, to enable a comparison of petrel distributions, location data were split into 3 colony-based time-periods. Complete colony-based distributions were analysed together as 'full period' distributions (N=23). Additionally, partially tracked colony-based petrels were divided into two time periods that represent a proxy for the early and late breeding season: the first 60 days of a petrel's return to Round Island (hereafter referred to as 'early period', N=85) and the last 60 days before departure on migration (hereafter 'late period', N=71) were analysed separately. A preliminary examination of the data from the geolocators did not provide evidence for a pre-laying exodus for the Round Island petrels, as has been recorded in other Procellariform species (Bretagnolle et al., 1991, Catry et al., 2009, Guilford et al., 2012, Madeiros et al., 2012). To investigate within-individual variability in distribution between colony-based periods, the 23 complete (full period) colony-based distributions were divided into early and late periods for each individual and both periods for the 23 individuals were analysed together.

Generating locations

Prior to analysis, light records were visually examined and processed with a semi-automated data cleaning script to remove shading noise in the recorded data (Appendix C, Chapter 3). Locations were generated from light and SST data collected by the geolocators using Thiebot and Pinaud's (2010) partial implementation of the modelling approach presented in the '`tripEstimation`' package in the programming environment R (Sumner and Wotherspoon, 2012, R Development Core Team, 2013).

Bayesian Mixtures Analysis

The intra-population variation in the colony-based distribution of the petrels was quantified using a Bayesian framework developed by M.A.C. Nicoll and G. Holloway (*submitted)* The Bayesian Mixtures Analysis (BMA) allows individuals to be grouped

purely by similarities in the distribution of their location estimates in space, without using a priori classification of the individuals by an observer, i.e. by sex or population. Instead, regions of space are delineated by the observer and the number of location estimates in each region is counted and compared between individuals, and individuals are grouped based on similarities and differences in distribution with others in the BMA. For this study, the area in which petrel locations were recorded during their colony-based period was divided into regions based on sea floor bathymetry (Schott and McCreary Jr, 2001, Parson and Evans, 2005), delineating regions based on outlining ridges and basins. Details regarding the division of space and the counting of location points per individual within these divisions can be found in Appendix C (Figure 20).

Mapping

Petrels were mapped together at different spatial and temporal scales, with the following groupings; the whole dataset (all locations), colony-based periods (full, early and late) and mixtures within the colony-based periods (Table 2). The distribution of location points in each group were visualised using 95% (range) and 50% (core) kernel density estimations (KDE), to represent the general area covered (following Paiva et al., 2013, Gutowsky et al., 2015). These broadly grouped distribution estimates were then compared with the combined areas of sub-divisions within each group. The core polygons of the full, early and late periods were amalgamated to create a combined core area for different time periods and contrasted to the core area from the whole dataset (all locations, Table 2). Similarly, the core areas of each mixture within a colony-based time period were combined and contrasted to the core area of the colony-based period (Table 2).

Table 2: Groups: the area of ocean (km^2) encompassed by core polygons calculated for all locations, and for full, early and late colony-based period locations. Sub-divisions: the areas represent total ocean surface covered by the combined core areas of each subdivision within the group. The area omitted is the area covered by the combined polygons within a grouping that is not included in the area calculated from the whole group assuming no variation within it.

Group	Core area (km^2)	Sub-division	Combined sub-division core areas (km^2)	Area omitted (%)
All locations	564886	Full, Early and Late periods (N=3)	786920	28.2

Full period	558487	Full period mixtures (N=5)	1070898	47.8
Early period	482364	Early period mixtures (N=14)	2368488	79.6
Late period	540637	Late period mixtures (N=13)	1857829	70.9

4.4. Results

Population-level distribution of Round Island petrels

The distribution pattern of petrels based at Round Island is similar between the full period (Figure 11b) and the late period (Figure 11d), when compared to the distribution of all the petrel locations collected in the study (Figure 11a), and are of a similar size (Table 2). In contrast, during the first 60 days of their return to Round Island (early period) the petrels focused more to the south of the island in the Mascarene basin (Figure 11c), in a more concentrated area. Core areas used during the full and late period distributions were mostly encompassed by the core area identified using all locations (Figure 11b and d), but the early period distribution was less well represented by the overview of the whole distribution (Figure 11c).

Combining the core areas of each colony-based period resulted in a larger area than the core area generated using all the location estimates in a single calculation, with 28.2% of the combined area falling outside the single core area (Table 2). This combined area, unlike the whole dataset core area, assumes variation in colony-based distribution between colony-based periods.

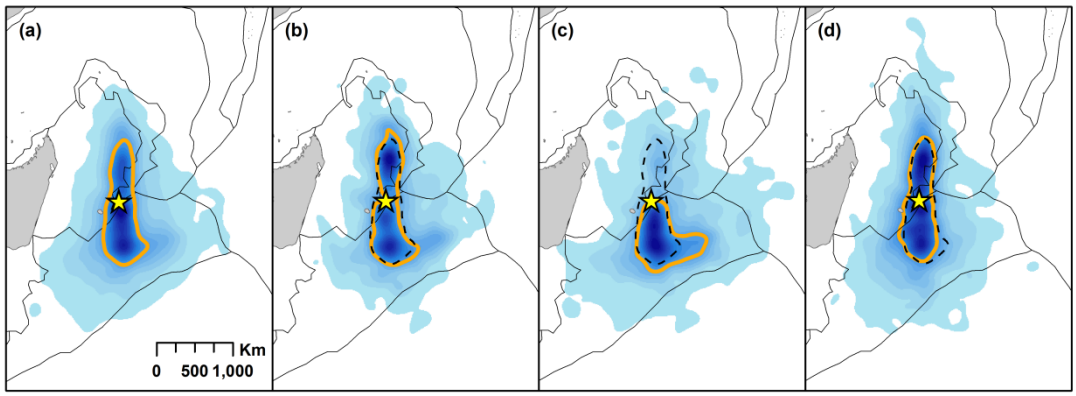

Figure 11: Kernel density estimations of all locations (a) and each of the three analysed time periods at Round Island, full period (b), early period (c), and late period (d). The 95% range estimates are represented in blue. The orange isopleth line shows the 50% density boundary, indicating the core

foraging distribution area in each time period. The dashed isopleth line represents the core distribution area (50% density) of the whole dataset. Solid black lines show boundaries to the bathymetry regions used in the BMA.

Individual-level variation in distribution patterns within colony-based periods

If no significant intra-population variation was present within the data, the BMA would have generated a single mixture to which all individuals would have been assigned. However, for each of the analyses, significant intra-population differences were detected.

The BMA identified 5 mixtures within the 23 individual distributions across the full Round Island-based period, each of which included between three and nine individuals (Figure 22). The combined core areas of the five mixtures covered an area around the colony roughly the shape of the overall area for the full period (Figure 12b), but was larger; 47.8% fell outside the overall core area.

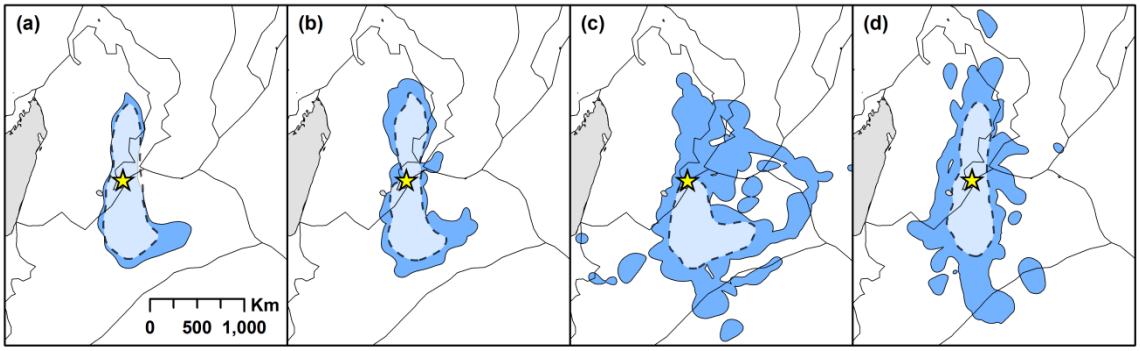

Figure 12: Overlaps between core foraging distributions (50% density) identified using the complete (translucent white with dashed outline) and sub-divided (blue) datasets. (a) The full dataset including all locations, and sub-divisions by time-period at Round Island (Full, Early and Late). (b) The full breeding period and the 5 full period mixtures. (c) The early period and the 14 early period mixtures. (d) The late period and the 13 late period mixtures. Solid black lines show boundaries to the bathymetry regions used in the BMA.

In the early colony-based period, 14 mixtures were identified in the 85 individual distributions, with a range of two to 31 individuals per mixture (Figure 23). The largest mixture of 31 individuals represented 36% of all the individuals included in this time period (Figure 13a). Important areas were highlighted in many different bathymetric regions, since the core areas of mixtures with two individuals were treated in the same way to mixtures including up to 31 individuals. Consequently, 79.6% of the area identified by combining the core areas of early period mixtures was not included in the total early period core area (Figure 12c, Table 2).

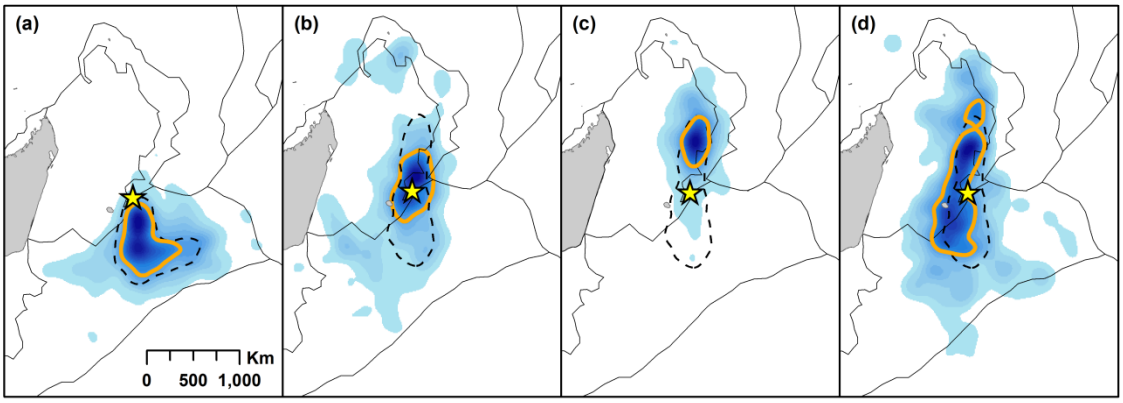

Figure 13: The largest mixtures in terms of number of individuals from the early ((a), N=31) and late ((b-d), N=8) colony periods. The range and core distribution estimates are represented as in Figure 11. The dashed isopleth line represents the core distribution area (50% density) of the all the locations in each period. Solid black lines show boundaries to the bathymetry regions used in the BMA.

Fewer mixtures were identified in the late period (13 mixtures in 71 individual distributions, Figure 24), however the range of individuals per mixture was more evenly spread in this time period, ranging from three to eight, with the three largest mixtures all containing eight individuals (Figure 13b, c, d). Similarly to the full and early colony-based periods, the overall late period core area did not adequately represent the variation within the season, with 70.9% of the combined mixture core area occurring outside the original core area (Table 2).

Within-individual variation across colony-based periods

The location estimates for 23 individuals that had full colony-based periods were divided into early and late period distributions for each individual, and both periods for each were analysed in the BMA together. From these distributions, eight mixtures were identified (Figure 25), but none of these mixtures included both the early period and late period distribution from the same petrel.

4.5. Discussion

In this study, marine areas of key importance to the unusual hybrid population of gadfly petrels on Round Island when based at the colony were identified for the first time. In addition, it was observed that population-level distribution estimates did not adequately represent the variation in the population at a temporal, between-individual or within-

individual scale. At a population-level, petrels appeared to predominantly visit parts of the Mascarene and Madagascar basins that were close to the colony, but accounting for intra-population variability in distribution greatly increased the core area used by the petrels in comparable colony-based seasons. Individual petrels were also shown to be inconsistent in their distributions between colony-based seasons.

Although this study includes petrels tracked throughout the year (Figure 21), the data collected is representative of a particular segment of the population that visit Round Island, which may have led to an underestimation of the variation present within the population. This is because geolocators were deployed on petrels between November and February, a period of the year when petrel attendance at Round Island is at its highest (Tatayah, 2010). Therefore, variation in distribution is measured predominantly between June and August, and numbers of petrels tracked between February and May are low (Figure 21). Even greater overall variation may have been discovered if petrels were caught and tagged outside the peak season, when conditions in the marine environment around the island are likely to be different, and this would be a valuable direction for further research. Alternatively, variation within comparable colony-based periods may have been overestimated due to the difficulty in ascertaining the exact breeding stage of individual petrels. Petrels in this study were assigned to a colony-based period, with the aim of grouping petrels at similar stages in their annual cycles, however it is likely that some petrels in these groups differed in their breeding status. It is assumed that petrels returning to the colony are doing so to breed; however, it is likely that while some may be raising young, many do not mate or are involved in failed breeding attempts. Therefore, petrels within a period may not be breeding, or alternatively may incubating an egg or be provisioning a chick, causing there to be different demands and constraints for foraging around the colony (Huin, 2002, Hyrenbach et al., 2002, Weimerskirch et al., 1993, Ramírez et al., 2013). This would result in an overestimation of the intra-population variation observed.

Results of the BMA, in terms of the optimum number of mixtures that describe variation in the data and the assignment of individuals to those mixtures, are strongly influenced by the division of space chosen by the observer. In this study, the ocean area was divided using bathymetric features (Figure 20). Seabird distributions are often described in terms of ocean-floor topography (Hyrenbach et al., 2002, Yen et al., 2004, Catry et al., 2009, Freeman et al., 2010, Pinet et al., 2011a), as these affect the marine food web and therefore prey availability to seabirds. Specifying fewer regions may reduce the power of the BMA to detect variation; likewise increasing divisions to small regions may reduce the actual differences in distribution between mixtures. Therefore it

is important that an ecologically meaningful division of space must be decided upon prior to the use of the BMA.

The core areas for all locations (Figure 11a), the full colony-based period (Figure 11b) and the late period (Figure 11d) were highly consistent and overlapping, so the population-level hotspot approach (Lascelles et al., 2012) would appear reasonable at this temporal scale. However, this distribution pattern contrasts with the early period, when the core foraging area is smaller (Table 2) and is focused entirely to the south of the island in the Madagascar Basin (50% kernel density estimate, Figure 11c). This area is also targeted by chick-rearing Barau's petrel (*P. baraui*) from the nearby colony at Réunion (Pinet et al., 2012b), and may therefore be a particularly valuable area to breeding seabirds. The population-level difference in the distribution of Round Island petrels across their time at the island at suggests that studies only investigating a single time period in a seabird's annual cycle may overlook important variation in distribution patterns.

Working with regions defined by seafloor features, the BMA identified substantial intra-population variation in all colony-based periods investigated. This is likely to be because prey availability around Round Island is low and patchily distributed, as is characteristic of oligotrophic tropical oceans (Ashmole, 1971, Ballance and Pitman, 1999), and therefore a flexible foraging strategy is favoured over consistent exploitation of a particular area (Weimerskirch et al., 2005b, Weimerskirch, 2007). Results from the BMA suggest that petrels are less variable in distribution during the early periods, because a greater overall proportion of all individuals in that time period were assigned to a single mixture (36%), which concentrated in the Madagascar basin (Figure 13a). In the first few months after returning from migration, petrels are more likely to be at the same stage in the breeding cycle and experiencing similar constraints, which may explain the reduced variation seen at this time. Alternatively, the Madagascar basin may present a predictable area of prey availability for petrels returning to the colony. In contrast to the early period, each of the three largest (in terms of individuals) mixtures in the late period included just 11% of the total number of individuals in the analysis (Figure 13b, c, d). Petrels present at the colony later in the colony-based period are more likely to be at different stages of their breeding cycles, due to nest failures and varying hatching dates and chick development, and therefore it is not surprising that more variation is seen during this period.

The combined core areas that described variation within a group were very different from the overall group they were derived from (Figure 12a-d, Table 2). The effect was smaller when comparing the combined core areas from different colony-based time

periods with the core area derived from all locations, with 28.2% of the population-level variation in core area falling outside the basic kernel density estimation (Figure 12a, Table 2). However, the difference in area becomes very large when considering the intra-population variation at a narrower temporal scale. By not taking into account this variation, between 47.8% – 79.6% of the core area visited by petrels is not identified in the kernel density estimations. This result complements the findings of Gutowsky et al. (2015), who demonstrate on two species of tropical albatross that due to individual variations in space-use, pooled KDE outputs may badly misrepresent population-level distributions, as they are strongly influenced by sampling effects.

In addition to between-individual variation in distribution around the colony, results showed that the early and late period distributions of individuals were not assigned to the same mixture when both were included in the same mixtures analysis. This suggests that, unlike many seabirds (Ceia et al., 2012, Cecere et al., 2013, Patrick and Weimerskirch, 2014, Potier et al., 2015, Ramírez et al., 2015, Patrick et al., 2013), individual petrels are not consistent in their distribution throughout the colony-based period and utilise more than one distinct area.

Many studies have looked into the factors that affect variability in seabird distribution patterns. These can be intrinsic, between-individual differences, such as sex (Ceia et al., 2012, Pinet et al., 2012b, Thiers et al., 2014, Quillfeldt et al., 2014, Weimerskirch et al., 2014), breeding stage (Pinet et al., 2012b, Cleeland et al., 2014, Weimerskirch et al., 1993), age (Péron, 2013, Thiers et al., 2014, Weimerskirch et al., 2014) and even personality traits (Patrick and Weimerskirch, 2014), or extrinsic, environmental factors such as inter-seasonal or -annual differences in prey availability (Paiva et al., 2010a), wind patterns (Weimerskirch et al., 2012) lunar cycle (Pinet et al., 2011b, Ramírez et al., 2013). The variability found in Round Island petrels may be an adaption to breeding in oligotrophic tropical regions, as during their migratory periods away from the colony in more seasonal oceans, Round Island petrels have been found to be individually consistent in their migratory distributions (Nicoll *et al. in submission*). Another factor that may attribute to the high level of variation seen within the Round Island petrel population is its hybrid status (Brown et al., 2010, Brown et al., 2011). The influence of the diverse genetic composition of this population on its distribution patterns is an interesting direction for future research.

Whatever the cause of such diversity in colony-based distribution, these differences may have an effect on individual survival and breeding success, and hence the long term survival of the population or species in the face of global change (Reed et al. 2010). Behavioural flexibility may bestow some individuals with a selective advantage

over others. For example, food abundance in a seabird's breeding range has a huge impact on breeding success, and long-lasting prey depletion in an area may have a negative impact on seabird population size (Cury et al., 2011). Some species can mitigate the impact on patchy or unpredictable resources on their breeding success or body condition by adopting a flexible foraging strategy (Weimerskirch et al., 2005c, Paiva et al., 2013, Deppe et al., 2014). However, individuals with varying distributions may also have a differential exposure to anthropogenic threats (Ceia et al., 2012, Le Corre et al., 2012, Ramírez et al., 2015), such as bycatch (Anderson et al., 2011), oil spills near shipping lanes (Le Corre et al., 2012) or ocean currents that collect plastic debris that may be accidentally ingested (Derraik, 2002, Spear et al., 1995). Additionally, prey availability within an individual's range may become less predictable as the effects of climate change impact marine ecosystems (Hoegh-Guldberg and Bruno, 2010).

Differences in distribution patterns may cause complicated interactions between positive and negative effects on seabird survival and productivity, both at an individual- and a population-level, and this is an important consideration to take into account when designating areas for marine protection. While it has been established that seabird ranges can be used to identify ecologically valuable regions for protection at a species- or colony-level (Lascelles et al., 2012, O'Brien et al., 2012, Ronconi et al., 2012), capturing the variability within the study population is critically important to provide sufficient protection for behavioural diversity, which may buffer a vulnerable population against future changes (Dias et al., 2013, Reed et al., 2010, Chirgwin et al., 2015). For some species with limited ranges, a population-level approach may provide adequate protection (Young et al., 2015). However, intra-population variability will be more pronounced in wide-ranging, highly mobile taxa, for example Procellariiformes (Gutowsky et al., 2015). Round Island petrel distribution likely reflects areas that are ecologically important to other marine biodiversity found in the Indian Ocean, which are predominantly un-protected from human pressures such as industrial fisheries and oil pollution. Biodiversity in the Indian Ocean could benefit from conservation planning measures that capture behavioural diversity and between individual, intra-population variability in distribution at a range of life-cycle stages, as demonstrated here.

Chapter 5: Colony-based distribution of tropical petrels influenced by seasonal climate, but not genotype

5.1. Abstract

Breeding seabirds are bound to their colony and as such are constrained to central place foraging. The factors that influence the colony-based foraging distributions of seabirds have received much study, but tropical systems are under-represented. In particular, little is known about how individual differences and environmental conditions influence distribution in the same system.

In this study a rare naturally occurring 'common garden' study system is used to explore both genetic and environmental effects on the colony-based distribution of a mixed-species, tropical petrel (*Pterodroma*) population. The petrels breeding at Round Island have an asynchronous breeding cycle and have previously been shown to have extensive individual variation in their distributions around the colony. However, the cause of this is as yet unknown.

Multinomial logistic regression was used to test the influence of the two seasons of the south-western Indian Ocean and individual membership to a parental species group generated from microsatellite genotyping analysis on petrel distribution patterns. Seabirds are known to vary their foraging behaviour to match the changing demands of breeding whilst at the colony, therefore petrel distributions were split into comparable time periods (early and late colony-based periods) and these were investigated separately.

Both early and late in a petrel's approximately 23 week residence at the colony, seasonal conditions influenced distribution around the island. Specifically for both early and late colony-based distributions, the season in which a petrel returned to the island from migration was influential. The likelihood of belonging to one of the potential parental species groups had no influence on the broad-scale distribution of colony-based petrels early or late in the colony-based period.

The results show that despite originating from different oceans, the petrel species present in the Round Island population show considerable adaptability in response to environmental changes, independently of differences in genotype. With environmental conditions becoming less predictable in the future of climate change, this flexibility may provide an evolutionary advantage to tropical seabirds.

5.2. Introduction

Seabirds are renowned for the huge distances they can cover across the oceans and are one of the widest ranging taxa in the world. However when based at their colonies, breeding seabirds are constrained by the need to meet the demands of self-provisioning while ultimately returning to a fixed location to incubate eggs or provision chicks, in a classic central place foraging scenario (Orians and Pearson, 1979).

The key factor that influences seabird distribution at any life history stage, but particularly at the colony is the surrounding availability of food, itself influenced by large-scale environmental conditions. Changes in prey availability to seabird colonies can be affected by sea surface temperature (Velarde et al., 2015, Jaquemet et al., 2007), chlorophyll *a* concentration (Devney et al., 2009, Jaquemet et al., 2007), oceanic upwellings (Lévy et al., 2007, Ainley et al., 2005) and wind conditions (Weimerskirch et al., 2012), for example. These variables are influenced by large scale climate phenomena (Devney et al., 2009), and their effects may vary from year to year. Interactions between environmental factors cause the distribution of resources in the ocean to be patchy and scale-dependant (Weimerskirch, 2007, Ashmole, 1971), but in temperate and polar regions, where environmental conditions undergo strong seasonal changes, prey resources are frequently predictable in their location and within easy reach of the colonies. This causes seabirds to target areas that are spatially and temporally predictable in terms of resources at a larger scale (Weimerskirch, 2007) and to adopt synchronous breeding cycles to match prey availability (Croxall and Prince, 1980, Frederiksen et al., 2004).

In contrast, tropical oceans are characteristically low in productivity and prey abundance (Ashmole, 1971, Ballance and Pitman, 1999, Ashmole, 1963), and lack a strong seasonality in environmental conditions which reduces the predictability of marine resources. As a result of this, many tropical seabird species have asynchronous breeding cycles (Le Corre, 2001) and are variable in their foraging distributions (Deppe et al., 2014, Pinaud and Weimerskirch, 2005b, Weimerskirch, 2007, Burke and Montevecchi, 2009), which is likely to be advantageous when foraging in oligotrophic and unpredictable tropical oceans (Hennicke and Weimerskirch, 2014, Sommerfeld et al., 2015, Sommerfeld and Hennicke, 2010, Gutowsky et al., 2015).

Such differences in distribution around the colony, be they spatial or behavioural, can often be seen between colonies of a single species, and may be a result of regional differences in prey availability (Rayner et al., 2008, Young et al., 2015, Wiley et al., 2012) or density of competitors (Oppel et al., 2015, Soanes et al., 2016, Wiley et al.,

2012). However, differences are also evident between sympatric species at a single colony. To reduce strong competition for resources from other seabirds at the colony (Lewis et al., 2001, Ashmole, 1963), different species or sub-species in a seabird community can adapt to target distinct prey types and regions (Pinaud and Weimerskirch, 2007, Hyrenbach et al., 2002, Navarro et al., 2009d, Kappes et al., 2011, Navarro et al., 2014, Weimerskirch et al., 2009, Young, 2010, Young et al., 2015), resulting in different at-sea distributions around their colonies.

Even within a single population of the same species, the oligotrophic conditions of tropical oceans may mean that it is not profitable for all individuals to exploit the same foraging locations (Oppel et al., 2015). Substantial variations in colony-based foraging distributions are commonly seen between individuals at different stages of their breeding cycle, due to changes in the energetic demands of raising a chick (Weimerskirch et al., 2004, Mendez et al., 2016, Navarro et al., 2014). Sex differences in distribution have also been demonstrated in species with sexual dimorphism or with different energetic constraints whilst breeding (Pinet et al., 2012b, Weimerskirch et al., 2009, Weimerskirch et al., 2006a) and between individuals with differing levels of experience (Fayet et al., 2015). In addition, seabirds have been shown to adjust their foraging distributions in response to inter-annual changes in environmental conditions (Deppe et al., 2014, Hennicke and Weimerskirch, 2014, Mendez et al., 2016).

While colony-based distribution has been studied from a large number of angles, tropical seabirds are still under-represented in the literature, and to date quantifying the extent of within-population variation in tropical systems has been very limited (see Chapter 4). As yet no study has attempted to explore how quantifiable differences between individuals might shape their distribution patterns alongside larger seasonal differences in the surrounding environment.

This study therefore presents a timely and unique opportunity to explore the influence of both genetic and environmental factors on the colony-based distribution patterns of a population of tropical gadfly (*Pterodroma*) petrels breeding on Round Island (hereafter referred to as 'Round Island petrels'), off the coast of Mauritius in the south-eastern Indian Ocean. Large scale tracking studies have shown that Round Island petrels have extensive individual variation in distribution at sea both when colony-based (Chapter 4) and during migration (Nicoll *et. al. submitted*), however the cause of this is as yet unknown.

The Round Island population is particularly interesting as it represents a naturally occurring 'common garden' experiment. The population consists of at least three

species of Pterodroma originating from the Atlantic (Trindade petrel, *P. arminjoniana*) and Pacific (Kermadec petrel, *P. neglecta* and Herald petrel, *P. heraldica*) Oceans, and contains two-way and three-way hybrids of these three species (Brown et al., 2011, Chapter 2, Brown et al., 2010). It is therefore a novel system in which to examine whether individuals of different genotypes distribute themselves differently around their breeding colony when experiencing the same set of environmental conditions. Originating in distinct ocean regimes, it would be expected that parental species show adaptations to the local conditions in which they evolved (Rayner et al., 2011, Friesen, 2015, Wiley et al., 2012, Silva et al., 2016), and that hybrids may inherit parental behaviours or intermediate behaviours (Delmore and Irwin, 2014). This could result in distinct foraging distribution strategies around the Indian Ocean colony. Alternatively, because the three species breed in sympatry at the same colony, segregation of foraging distribution may reduce inter-specific competition for prey.

In addition to their between-individual genetic differences, Round Island petrels have an asynchronous breeding period, in common with other tropical species. Consequently, individuals may experience different environmental conditions when based at the colony, which may influence the distribution of prey in the surrounding ocean and hence the foraging distribution of the petrels (Deppe et al., 2014, Hennicke and Weimerskirch, 2014, Mendez et al., 2016).

In this study, multinomial logistic regression analysis was used to test whether or not the demonstrable variation in the colony-based distributions of Round Island petrels arises through individual differences, measured using the probability of membership to a parental species group generated from microsatellite genotyping analysis (Chapter 2), or the wider seasonal environment as characterised by the two main seasons of the tropical south-western Indian Ocean. The distribution patterns of colony-based petrels were investigated at two contrasting time periods in a petrel's annual cycle: the first two months of arrival at the island, and the last two months before departing on migration. This is because breeding stages have been shown to be important in determining seabird colony-based distribution patterns (Weimerskirch et al., 2004, Mendez et al., 2016, Navarro et al., 2014).

5.3. Methods

Tracking

Round Island petrels were caught during routine seabird monitoring by the Mauritius Wildlife Foundation warden team at their breeding colony on Round Island (19.85^{o} South, 57.78^{o} East). Between November 2009 and February 2011, 220 petrels were fitted with Mk 15 geolocators (British Antarctic Survey). For full details of the geolocation procedure and the generation of location estimates from geolocation data see Nicoll et al. (2016). The return dates of petrels to the island from migration, and subsequent departures for the next migration, were identified by visually inspecting light and immersion data. Tracked periods at the island that exceeded 60 days, referred to as the 'colony-based periods', were selected for further study (for details see Chapter 4). From the total geolocation deployment, 116 tags were retrieved with useable data, and of these 95 contained at least one colony-based period exceeding 60 days.

Analysis of distribution data

To enable a fair comparison of colony-based distributions, they were split into two comparable time periods when the petrel was present at the colony: the 'early period', the first 60 days after returning from migration (N = 76) and the 'late period', the last 60 days spent at the island prior to leaving on migration (N = 65). Early distributions and late distributions were analysed separately in a bespoke Bayesian Mixtures Analysis ('BMA', detailed in Chapter 4) to group petrels into 'mixtures' by spatially similar distributions. In the early colony period, 14 distinct mixtures were identified, and in the late colony period, 13 mixtures were identified. To enable the explanation of distribution patterns with a limited sample size, mixtures were aggregated in each time period into three categories, based on the focal locations of the 50% kernel density estimations (core area, following Paiva et al., 2013, Gutowsky et al., 2015) in each mixture with regards to Round Island (Figure 26, Table 11). For methods of kernel density estimation, see Chapter 4. The categories were 'South Only' (SO), North Only' (NO), and 'North-South' (NS, occurring in both).

Seasons in the south-west Indian Ocean

The climate of Mauritius and the surrounding ocean can be divided into two broad seasons: the austral winter (1st May - 30th September) and the austral summer (1st October - 30th April) (Jury and Pathack, 1991, Le Corre, 2001, Staub et al., 2014). The unequal split in the months reflects the influence of the monsoon circulation of the Indian Ocean, where the south-western monsoon dominates from approximately May to September and the north-eastern monsoon from October to April. This weather phenomenon is characterised by semi -annual wind reversals in the northern Indian Ocean (Schott and McCreary Jr, 2001, Lévy et al., 2007, Wiggert et al., 2006), and these cause changes to ocean circulation, upwellings and vertical mixing (Lévy et al., 2007, Wiggert et al., 2006), consequently effecting ocean productivity and hence prey availability for marine life. An easterly trade wind prevails throughout the year in the south-western Indian Ocean, but the strength of this is lessened in the summer months (Schott and McCreary Jr, 2001). During the winter months the sea surface temperature is lower (Le Corre, 2001) and the surface chlorophyll a concentration (a marker of ocean productivity) is higher (Wiggert et al., 2006).

Changes in the environmental conditions around Round Island were therefore expressed in this study using the two basic seasons that dominate the climate of Mauritius: austral winter (hereafter 'winter') and the austral summer (hereafter 'summer'). These two seasons were included in the analysis in two ways: the first recorded the season relative to the timing of the tracked period of the petrel as a two-level variable, summer or winter (season: S or W). The second looked for evidence of inter-annual variation in the effect of the seasons on petrel distributions by recording the season as a combination of the two seasons and the three years of tracking (2009/10, 2010/11, 2011/12), creating a six-level variable ('season-year': W_09, S_09, W_10, S_10, W_11, S_11. i.e. W_09, winter starting in 2009). The season was recorded for the start of the early colony tracking period, when the petrel arrived at Round Island from migration, to reflect environmental conditions which it was experiencing during tracking. However, the season was calculated at two dates for petrels tracked in the late colony period: the beginning of the tracked period ('season-late', or 'season-year-late'), and the arrival date of the petrel to Round Island ('season-arrival', or 'season-year-arrival'). The arrival date was known for 23 of the 65 petrels tracked in the late colony-based period, and on average was 23 weeks from its subsequent departure on migration. However, 42 individuals tracked during the late period did not have a known arrival date at Round Island. To calculate the season in which these individuals arrived at Round Island, the average duration of the colony-

based period (23 weeks) was subtracted from the known departure date, and this was then used to find the season in which they arrived. This method was tested on individuals with a known arrival date, and it was found that in 96% of cases, the correct arrival season was calculated as a result.

Genetic background

Petrels fitted with geolocators were also blood sampled, and of the 95 petrels tracked at the colony, 72 were successfully genotyped using a suite of 12 microsatellite markers (59 individuals with early colony period distributions, 50 with late colony period distributions). Round Island petrel genotypes were analysed with genotyped individuals from potential source populations (Trindade Island and islands representing the Pacific ranges of Kermadec, Herald, Phoenix (*P. alba*) and Murphy's (*P. ultima*) petrels), using the using the clustering software STRUCTURE v.2.3.4. (Pritchard et al., 2000, Falush et al., 2003). Results from the STRUCTURE analysis suggested that the most likely number of genetic clusters across the genotyped petrel populations was four, and these groups largely reflected species groups, with the exception of Round Island. These clusters were: Trindade-type petrels, Kermadec-type petrels, Herald- or Phoenix-type petrels and Murphy's-type petrels. The analysis provided estimated membership (*Q*) values for each individual to each cluster, summing to a probability of one. The *Q* value of each individual to the Trindade-type cluster was used as a measure of genetic background for Round Island petrels in the analysis of their distribution patterns, as estimated memberships to each cluster are not independent. Full details of the genotyping and genetic analysis methods can be found in Chapter 2.

Statistical analysis

The '`multinom`' function in the R package '`nnet`' (Venables and Ripley, 2003, R Development Core Team, 2013, ver. 3.1.2.) was used to predict the likelihood of a petrel distributing in a pattern that fit one of the three possible distribution categories (SO, NO or NS) in each colony-based time period. This function fits a multinomial logistic regression model, suitable to the data since the dependent variable (petrel distribution) is a categorical variable of several distributional 'states' in which an individual might be potentially classified. Using multinomial logistic regression, the analysis therefore modelled the probability that an individual fell into each of the distributional states as a function of a set of predictor variables that reflected individual

and environmental effects. The predictor variables tested for influence on the distribution category were: genetic assignment (Trindade-type *Q,* continuous), sex (two-level factor, categorical), season (two-level measure of seasonal conditions, categorical) and season-year (six-level measure of inter-annual seasonal conditions, categorical). Sex was included along with the variables of interest, as male and female seabirds can sometimes adopt differing foraging strategies whilst involved in a breeding attempt (Pinet et al., 2012b). Season and season-year variables were considered for both the arrival date and the start of the tracked period for the late colony based period, and for the arrival date only in the early colony period. In a multinomial logistic regression, probabilities of parameters are estimated compared to a baseline category. In this study, the probability of a petrel choosing a NO or NS distribution was calculated with reference to the probability of a petrel choosing a SO distribution. Candidate models were constructed for all possible combinations of the independent variables, including interaction models, and the most parsimonious model was selected based on Akaike's Information Criteria (AIC) (Burnham and Anderson, 2003). Goodness-of-fit was evaluated using likelihood ratio tests by ANOVA (R Development Core Team, 2013).

5.4. Results

Influence of genetic background on distribution

Using the subset of individuals tracked during the early and late colony-based periods for which genotyping data was available, multinomial logistic regression analysis revealed that the inclusion of genotype (assignment to the Trindade-type cluster, *Q*) had no significant effect on improving the fit of the model over the null model (Table 3. Early Model 1.13 vs 1.14: $LR_{116, 114} = 1.18$, $P > 0.05$. Late Model 3.1 vs 3.10: $LR_{98, 96} = 0.68$, $P > 0.05$). All further analysis was therefore carried out on the full datasets for both early and late time periods, including individuals with no genotype data.

Table 3: Multinomial logistic regression models (ordered by AIC) for testing influence of genotype (as measured by assignment to the Trindade-type cluster in STRUCTURE analysis), season ('season' = two level monsoon measure, or 'season-year' = six level seasonal measure, incorporating inter-annual differences over three years), and sex on the probability of a individual belonging to one of three distribution categories (South Only, North Only or North and South). RD = residual deviance of the model, ΔAIC = the difference between the AIC of the top model and the current model. Models above the dotted line have ΔAIC <2 from the top model.

Colony period and dataset	Model	Model predictors	RD	AIC	Δ_{AIC}
Early: Genotype (N = 59)	1.1	season	76.6	84.6	0.0
	1.2	season-year	65.4	85.4	0.8
	1.3	Trindade + season-year	63.3	87.3	2.7
	1.4	Trindade + season	75.6	87.6	3.0
	1.5	season + sex	76.6	88.6	4.0
	1.6	season-year + sex	65.4	89.4	4.8
	1.7	Trindade * season	74.3	90.3	5.7
	1.8	season-year + sex + Trindade	63.2	91.2	6.6
	1.9	season + sex + Trindade	75.6	91.6	7.0
	1.10	season * sex	76.6	92.6	8.0
	1.11	season-year * sex	57.5	97.5	12.9
	1.12	Trindade * season-year	58.1	98.1	0.7
	1.13	null	95.6	99.6	15.0
	1.14	Trindade	95.6	102.4	17.8
	1.15	sex	95.6	103.6	19.0
	1.16	season * sex * Trindade	72.0	104.0	19.4
	1.17	Trindade + sex	94.4	106.4	21.8
	1.18	Trindade * sex	94.1	110.1	25.5
	1.19	season-year * sex * Trindade	52.2	116.2	31.6
Early: No Genotype (N = 76)	2.1	season	90.8	98.8	0.0
	2.2	season-year	81.2	101.2	2.4
	2.3	season + sex	88.5	104.5	5.7
	2.4	season-year + sex	78.3	106.3	7.4
	2.5	season * sex	88.5	108.5	9.7
	2.6	null	112.3	116.3	17.5
	2.7	season-year * sex	70.6	118.6	19.8
	2.8	sex	109.4	121.4	22.6
Late: Genotype (N = 50)	3.1	null	107.4	111.4	0.0
	3.2	season-late	104.3	112.3	0.9
	3.3	season-year-late	92.6	112.6	1.1
	3.4	season-arrival * sex	96.6	112.6	1.2
	3.5	season-arrival	105.6	113.6	2.2
	3.6	Trindade * season-late	97.6	113.6	2.2
	3.7	season-year-late + sex	90.3	114.3	2.9
	3.8	season-year-arrival	90.6	114.6	3.2
	3.9	Trindade	106.7	114.7	3.3
	3.10	sex	107.2	115.2	3.8

	3.11	Trindade + season-year-late	91.3	115.3	3.9
	3.12	Trindade + season-late	103.6	115.6	4.2
	3.13	season-late + sex	104.0	116.0	4.6
	3.14	Trindade + season-arrival	105.3	117.3	5.9
	3.15	season-year-arrival + sex	89.5	117.5	6.0
	3.16	season-arrival + sex	105.5	117.5	6.1
	3.17	Trindade + season-year-arrival	89.5	117.5	6.1
	3.18	Trindade * season-year-arrival	73.8	117.8	6.4
	3.19	Trindade + sex	106.6	118.6	7.2
	3.20	season-late * sex	102.8	118.8	7.4
	3.21	Trindade * season-year-late	82.9	118.9	7.5
	3.22	Trindade * sex	104.2	120.2	8.8
	3.23	season-year-late * sex	84.5	120.5	9.1
	3.24	Trindade * season-arrival	105.0	121.0	9.6
	3.25	season-year-arrival * sex	78.1	122.1	10.7
Late: No Genotype (N = 65)	4.1	season-year-arrival	108.6	132.6	0.0
	4.2	season-year-arrival + sex	101.0	133.0	0.3
	4.3	season-arrival	125.9	133.9	1.3
	4.4	season-year-late	114.9	134.9	2.3
	4.5	season-year-late + sex	108.1	136.1	3.5
	4.6	season-arrival + sex	121.7	137.7	5.1
	4.7	season-late	129.9	137.9	5.3
	4.8	null	135.6	139.6	6.9
	4.9	season-arrival * sex	115.6	139.6	6.9
	4.10	season-late * sex	126.8	142.8	10.2
	4.11	season-year-arrival * sex	84.9	144.9	12.3
	4.12	sex	133.0	145.0	12.3
	4.13	season-late * sex	126.2	146.2	13.5
	4.14	season-year-late * sex	100.7	148.7	16.0

Seasonal influence on early colony period distribution

The top model by AIC early in the colony-based period for Round Island petrels was Model 2.1 (Table 3), which explained a petrel's chosen distribution category using the seasons without inter-annual differences. The model coefficients are shown in Table 12, and show the change in log odds of a petrel distributing to the north of Round Island or between the north and the south, relative to choosing a southern distribution, during different seasons. Predictions made by the model are represented in Figure 14A, which shows that NO distributions are only likely in the summer season, NS distributions are equally likely in both the summer and winter and the likelihood of a SO distribution decreases from 0.76 to 0.25 if switching from winter to summer (Table 16).

The spatial distribution of petrel locations is visualised with kernel density maps in Figure 15, and shows that petrel distribution is more concentrated to the south of Round Island in the winter (Figure 15A) than in the summer (Figure 15B).

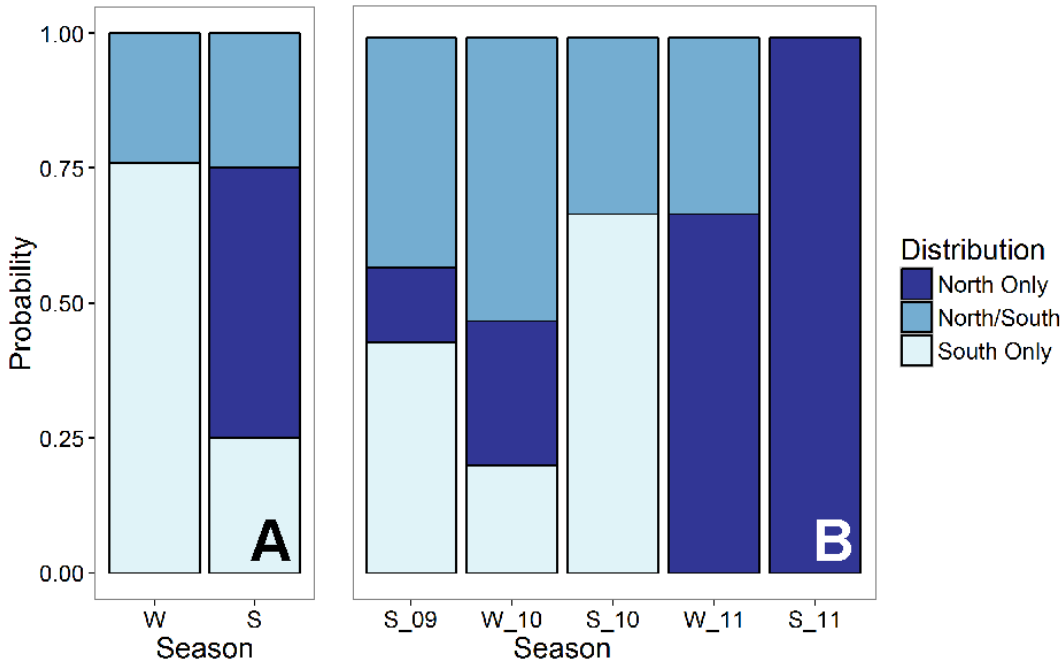

Figure 14: A: Predicted probabilities of petrel distribution in the early colony-based period relative to the monsoon conditions in which they arrive at Round Island (W = winter, 1st May to the 30th September; S = summer, 1st October to the 30th April). B: Predicted probabilities of petrel distribution in the late colony-based period relative to the inter-annual seasonal conditions in which they arrive at Round Island (e.g. W_09 = the winter of 2009. Years span 2009/10 to 2011/12).

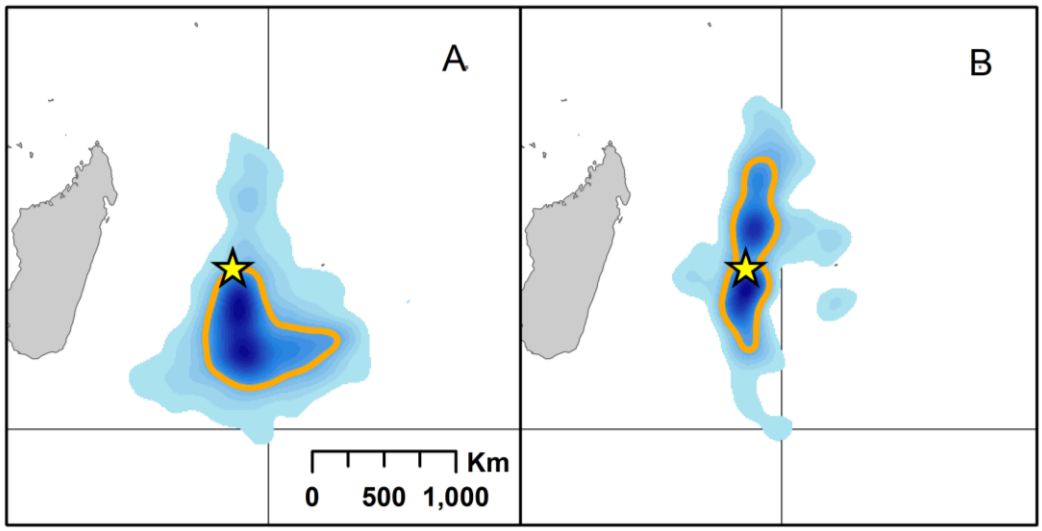

Figure 15: Round Island petrel distribution differences (90% range density = blue kernel; 50% core density = orange isopleth line) between the winter (A) and the summer (B) in the early colony-based period.

Seasonal influence on late colony period distribution

The season in which petrels arrived at Round Island had a greater effect on the fit of the multinomial logistic regression models than the season it was tracked in late in the colony-based period (Table 3, Model 4.1 vs Model 4.4). However unlike the early period, including inter-annual differences in the seasonal differences significantly improved the model fit over the two-level seasonal measure (Table 3, Model 4.1 vs Model 4.3: $LR_{126, 118} = 17.26$, $P < 0.05$). The coefficients of the top model by AIC, Model 4.1 are shown in Table 14, and predictions from the model are shown in Figure 14B. NS distributions were more likely for petrels in the late colony-based period if they arrived at Round Island in the winter, but the likelihood of having a NS distribution decreased from 2009 to 2011 (Figure 14B, Table 17). Conversely, SO distributions late in the colony-based period were more likely if petrels arrived in the summer, and this effect increased from 2009 to 2010. No petrels were tracked using a NS or SO distribution in the summer of 2011. The kernel density maps in Figure 16 show the late period distributions of petrels that arrived at Round Island in different seasons and years. In consecutive seasons S_10 (N = 9) and W_11 (N = 9) there is a clear shift from a southerly focused distribution to a northerly distribution.

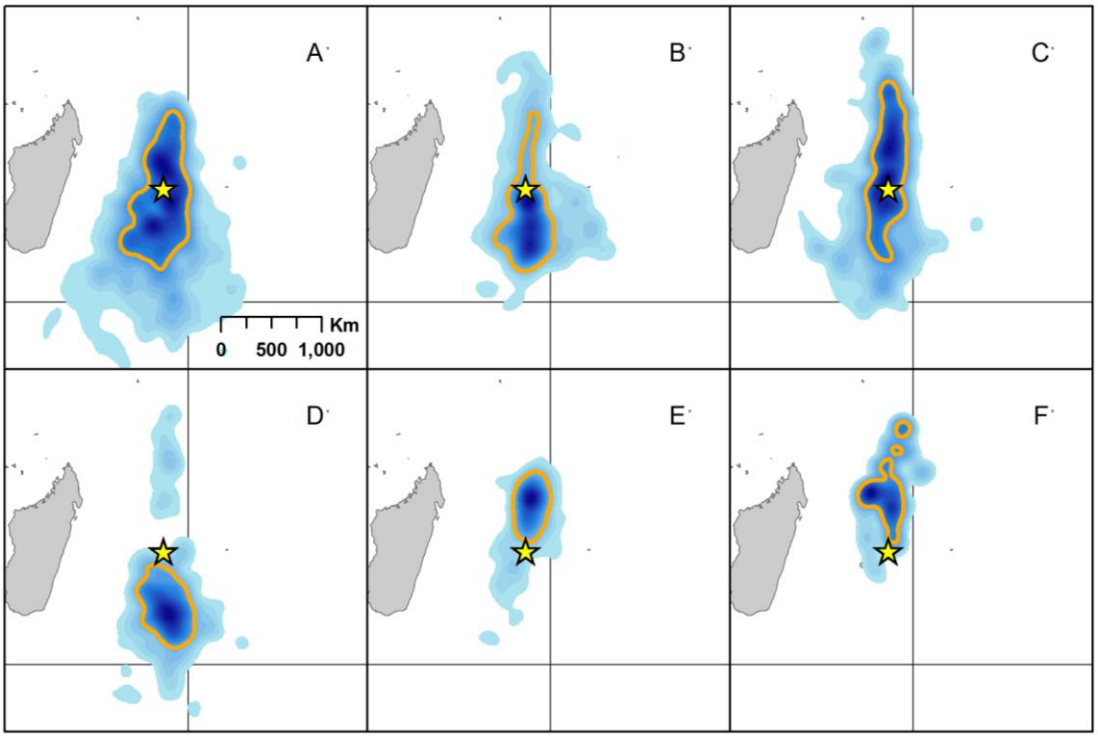

Figure 16: Late colony-based distribution differences (90% range density = blue kernel; 50% core density = orange isopleth line) between petrels that arrived at Round Island in the winter (A, C and D) and the summer (B, D and F) between years (A and B = 2009/2010, C and D = 2010/2011 and E and F = 2010/2011).

Influence of sex difference on colony-based distributions

Although the inclusion of sex as an independent variable did not improve the overall model fit for petrels early in the colony-based period (Table 3), in the late period, the model that included the variables 'season-year-arrival' and 'sex' (Model 4.2) fell within 2 AIC units of the top model, 4.1 (season-year-arrival). These two models were not significantly different in their goodness-of-fit (Model 4.1 vs Model 4.2: $LR_{118, 114} = 7.68$, $P > 0.05$). However, including 'sex' as the sole independent variable does not improve the fit of the model over the null (Table 3).

5.5. Discussion

This study is the first of its kind to explore both genetic and environmental influences on the broad-scale distribution patterns of colony-based seabirds in a tropical ocean. Despite the diverse genetic background of the population of *Pterodroma* petrels studied, genetic similarity to a parental species, Trindade petrel, did not predict a petrel's distribution around the colony. Both early and late in a petrel's approximately 23 week residence at the colony, seasonal conditions appeared to influence distribution around the island. Specifically for both early and late colony-based distributions, the season in which a petrel returned from migration was influential on its distribution patterns in the first 60 days of its time at the colony, and in the last 60 days before it leaves on a subsequent non-breeding migration.

Although the analysis presented here was able to explore the relative influence of genetics and environment on petrel distribution around Round Island, as for many tracking studies, the sample size was necessarily limited. To efficiently deploy geolocators onto petrels tagging mainly occurred on Round Island between November and February, when numbers of petrels are highest at the colony (Tatayah, 2010). This led to more birds being tracked in the winter (early period, N = 68, late period, N = 41) than the summer (early period, N = 8, late period, N = 24), and subsequently some model outcomes did not include any data to analyse (early period: NO distribution in the winter. Late period: NO distribution in the summer of 2010, SO distribution in the winter and summer of 2011, and NS distribution in the summer of 2011, Table 17). As the maximum likelihood estimation method used by multinomial logistic regression requires large sample sizes to generate robust model predictions, the discussion here

focuses mainly on the effect variables had on improving the model fit over the null, rather than aiming to define distribution trends using model predictions.

It is surprising that genotype did not appear to be a predictor of distribution for colony-based Round Island petrels. The three known parental species present in the population evolved outside the Indian Ocean, likely under different ocean regimes, a factor thought to cause local adaptation and prevent mixing between species (Friesen, 2015). Additionally, previous research shows that seabirds breeding in proximity segregate their foraging areas to reduce inter-specific competition for resources (Wiley et al., 2012, Finkelstein et al., 2006, Navarro et al., 2009d, Wakefield et al., 2013, Navarro et al., 2013, Weimerskirch et al., 2009, Kappes et al., 2011, Wiggert et al., 2006, Young et al., 2015, Young et al., 2010, Navarro et al., 2014). This is thought to be especially true of seabirds foraging in oligotrophic oceans, like the tropical Indian Ocean, where resources are few and far between, as opposed to super-abundant areas (Forero et al., 2004). However, this result agrees with the findings of a study on the spatio-temporal distribution of three cryptic species of gadfly petrel (*P. madeira, P. deserta* and *P. feae*) breeding in the Macaronesian islands of the Atlantic Ocean. Ramos et al. (2016) found that these three species of petrels breeding in proximity shared common foraging areas and strategies during their breeding seasons, and posited that the lack of spatial and behavioural segregation between the species was due to their very small population sizes, leading to an absence of inter-specific competition. This may also be true of the Round Island population, which is estimated to have a population size of 1400-1500 individuals (M.A.C. Nicoll, *unpub. data*). Another explanation for the lack of spatial segregation seen between species in the Round Island population may be because recent research suggests that Round Island petrels are very flexible in their distribution strategies at sea, both during migrations (Nicoll *et al. submitted*) and when colony-based (Chapter 4). This behavioural flexibility may have evolved as an adaptation to oligotrophic tropical environments and may be common to all the species.

Findings that Round Island petrel distributions are influenced by environmental conditions dictated by the two broad seasons of the south-western Indian Ocean are consistent with the patterns seen in other seabird species. Within the Indian Ocean, Barau's petrels (*Pterodroma baraui*) from the nearby island Réunion take advantage of wind conditions and seasonal phytoplankton blooms in their wintering migrations (Pinet et al., 2011a), and the breeding distributions of wedge-tailed shearwaters (*Ardenna pacifica*) from the Seychelles match local blooms linked to the monsoon circulation during the austral summer (Catry et al., 2009). Also in the Indian Ocean, yellow-nosed

albatross (*Thalassarche chlororhynchos*), Abbott's boobies (*Papasula abbotti*) and Red-footed boobies (*Sula sula*) vary their foraging distributions during the breeding season to adjust for changes in environmental conditions (Pinaud et al., 2005a, Hennicke and Weimerskirch, 2014, Mendez et al., 2016). Outside the Indian Ocean, the effect of changing environmental conditions on the breeding distributions of tropical seabirds appears to have received little scientific attention. However , in temperate oceans inter-annual fluctuations in the North Atlantic Oscillation (NAO) index have been shown to coincide with changes in the foraging range of breeding northern gannets (*Morus bassanus*) (Warwick-Evans et al., 2016).

Unlike many studied seabirds, which are often temperate or polar species relying on temporally and spatially predictable resources, Round Island petrels are asynchronous breeders (Tatayah, 2010). This causes individuals in the population to be exposed to different environmental conditions whilst present at the colony. This may explain why Round Island petrels show such a high level of intra-population variability in distribution (Chapter 4). This study shows that the season in which a petrel arrives at Round Island for its colony-based period, likely for a breeding attempt, is a predictor of both its distribution early and late in its time on the island.

When a seabird returns from migration to its breeding colony, it may either pair up and produce an egg or remain at the island without breeding. Some seabird species depart on a pre-laying exodus before incubation (Taylor et al., 2012, Rayner et al., 2012, Paiva et al., 2013), however there is no evidence of this in tracking data from Round Island petrels (*unpub. data*). Pairs that successfully produce an egg will share incubation (Brooke, 2004, Tatayah, 2010), and Round Island petrel eggs hatch at around 60 days old (Tatayah, 2010). Therefore, during the early colony-based period tracked petrels are either foraging at sea while their partner is incubating or not currently breeding and thus not closely tied to the island (incubating petrels shade their geolocators and cannot be tracked on incubation days, Chapter 2). Petrels early in the colony-based period are therefore able to make longer journeys away from Round Island and are able to exploit profitable areas of ocean not necessarily nearby (Weimerskirch et al., 1993, Huin, 2002). Although productivity in the ocean around Round Island is typically low throughout the year (Tatayah, 2010), chlorophyll *a* increases around August (during the austral winter) in the ocean to the north of the region (Wiggert et al., 2006). However, as can be seen in Figure 14A and Figure 15, during the winter petrels early in their colony-based period do not target areas to the north of Round Island, and are more likely to visit this area during the summer (October to April). This suggests that elevated levels of primary productivity, influenced by

seasonal changes (Lévy et al., 2007), may not immediately cause an increase in prey availability in these areas. Instead there may be a lag between primary productivity and an increase in prey (Durant et al., 2007, Monticelli et al., 2007).

In Chapter 4 it was demonstrated that petrel distribution at all stages of the colony-based period showed considerable variation in their at-sea distributions, but petrels in the late colony-based period varied more in their distribution patterns than in the early period. This may occur because petrels tracked late in the colony-based period are less likely to be at comparable stages of their annual cycle. Some petrels will have successfully bred, some will have had a failed breeding attempt, and some may not have bred at all. The results of this study suggest that this variation may be influenced by environmental conditions. Although models including the season in which petrels in the late-period were tracked did improve model fit over the null (Table 3, Models 4.4 and 4.7), the season they returned to Round Island in had a greater predictive power to explain late period distribution (Table 3, Model 4.1). Environmental conditions have a strong influence on the breeding success of many animals, and this link is widely documented in seabirds (Weimerskirch et al., 2001, Croxall et al., 2002, Monticelli et al., 2007, Surman et al., 2012). If seasonal differences in environmental conditions influence breeding success and the strength of this relationship varies between years, this may affect whether a petrel is successful in raising a chick to provision late in the colony-based period. Petrels returning to the island in favourable conditions would be more likely to be successful in breeding, and would be more likely to be provisioning a chick later in the season, a factor known to restrict foraging distribution in seabirds (Weimerskirch et al., 1993, Hedd et al., 2001, Huin, 2002). Also, petrels returning to the colony from migration may be using information on conditions in their environment to change their distributions to target particular areas throughout the colony-based period, as is reported in other seabirds (Warwick-Evans et al., 2016, Hennicke and Weimerskirch, 2014, Deppe et al., 2014, Mendez et al., 2016).

The inclusion of sex as a variable when considering the effects of inter-annual seasonal differences on late period distribution patterns (Table 3, Model 4.2) also improved the fit of the model over the null, and did not significantly differ in its goodness-of-fit from the top model (Table 3, Model 4.1). The influence of the seasons on a petrel's distribution around the island late in the colony-based period may perhaps be mediated by its sex. However, this result is unexpected as sex-differences in the distribution of monomorphic seabirds with bi-parental care are very unusual (Phillips et al., 2011, although see Pinet et al., 2012a). Results showed that the inclusion of sex alone did not improve the model fit during either the early or late period, and therefore it

is unlikely that sex has a strong effect on Round Island petrel distribution and the more parsimonious model (Table 3, Model 4.1) is a stronger choice.

This study is the first to investigate the effects of genotype and large-scale environmental conditions on the colony-based distribution of tropical seabirds. Tropical seabirds, and in particular tropical petrels, remain understudied in the literature and few other studies have investigated the effect of inter-annual variation in environmental factors on the breeding distribution of tropical seabirds (but see Hennicke and Weimerskirch, 2014, Mendez et al., 2016). The findings of this study provide a rare insight into the complex interactions between biotic and abiotic factors on the lives of tropical seabirds. Notably, the results presented here highlight the importance of flexibility in the behaviour of marine predators in oligotrophic environments. Despite originating from different oceans, the species and hybrids present in the population of petrels at Round Island show considerable adaptability in response to environmental changes, independently of differences in genotype. With environmental conditions becoming less predictable in the future of climate change (Walther et al., 2002, Burrows et al., 2011) this flexibility may provide an evolutionary advantage to tropical seabirds.

Chapter 6: Discussion

6.1. Summary

Pelagic seabirds are of huge conservation concern. After albatrosses, Gadfly petrels (*Pterodroma* and *Pseudobulweria*) are by far the most threatened group of seabirds (Croxall et al., 2012). Of the 34 extant species of *Pterodroma* petrel, 68% are considered 'threatened' under IUCN criteria (Critically Endangered, Endangered and Vulnerable), with a further 8% Near Threatened (Birdlife International, 2016b). Pelagic seabirds are mostly classified as threatened or Near Threatened due to small population sizes, rapid population declines, or both (Croxall et al., 2012). Some of the major threats to *Pterodroma* are encountered at sea, for example bycatch, climate change and pollution, but despite this the at-sea distribution of many *Pterodroma* petrels remains a mystery (Croxall et al., 2012). This lack of basic information about *Pterodroma* petrels limits our ability to protect them from direct human-induced threats or long-term ecosystem-level changes. The research presented in this thesis represents a first look into the global dispersal and colony-based distribution of *P. arminjoniana*, *heraldica* and *neglecta,* using a well-studied model system in the Indian Ocean. Prior to my research, the possibility of the Round Island petrel being unique in the world as a point of secondary contact and introgression between three species of gadfly petrel had not been explored. In addition, although previous research had been conducted on the breeding biology and genetic background of the population, nothing was known about the breeding distribution of the petrels, how consistent within the population this might be, or how their distribution might be influenced by individual genetic differences or environmental conditions. The aim of this thesis was to address these gaps in our knowledge of the Round Island petrel and so contribute to our understanding of tropical seabird ecology.

I began this thesis by exploring the role of the Round Island petrel population in the context of the potential source populations of *Pterodroma*. Gene flow between populations of seabirds is often restricted by biological or physical barriers (Friesen, 2015, Friesen et al., 2007a), and therefore previous research assumed Round Island to be a unique instance of secondary contact between Atlantic and Pacific petrel species (Brown et al., 2011). In Chapter 2 I used a suite of 12 microsatellite markers to genotype individuals from the Round Island population alongside Trindade petrel samples from the Trindade Islands and from different islands across the Pacific ranges

of Herald, Kermadec, Phoenix and Murphy's petrels. In contrast to the previously held hypothesis, the *secondary contact model*, the results supported the *widespread gene flow model* as inter-ocean migrants and possible hybrids were identified in populations outside the Indian Ocean. This suggested that Round Island is not the only point of contact between tropical petrel species of the Atlantic and Pacific Oceans, but instead this dispersal and colony-switching may be more widespread than previously thought. Widespread gene flow may not have been identified in previous phylogenetic studies of *Pterodroma*, as these studies often rely on small sample sizes (Brooke and Rowe, 1996, Brooke et al., 2000, Brown et al., 2011, Brown et al., 2010, Rayner et al., 2011). The incidences of migrants and hybrids in petrel populations are rare, and therefore analyses on small samples sizes are unlikely to detect them (Meirmans, 2014). This is a factor that influenced my analysis in Chapter 2. Although the results of the STRUCTURE analysis suggested the occurrence of hybrids and migrants outside the Indian Ocean, BAYESASS analysis did not detect migration of individuals between either the Atlantic and Pacific populations, or from Round Island to either the Atlantic or Pacific Oceans, despite populations being sufficiently distinct to detect migrants in theory. Greater sample sizes from island populations in the Pacific Ocean particularly may have aided the detection of migration between these populations.

The implications of current gene flow and introgression between species of *Pterodroma* in different oceans are complex. Hybridisation can be detrimental to very rare populations, leading to reduced reproductive fitness (Allendorf et al., 2001, Rhymer and Simberloff, 1996, Grant and Grant, 1992) and a homogenisation of potentially valuable genetic diversity (Brown et al., 2011). Although the species studied in this thesis are not all very rare, Herald and Kermadec petrels are declining, Murphy's petrel is near threatened, Trindade petrel is classified as 'Vulnerable' and the Phoenix petrel is 'Endangered' (Birdlife International, 2016b). Should range shifts brought about by climate change (Grémillet and Boulinier, 2009, Hickling et al., 2006) cause an increase in contact and gene flow between species, a reduction in fitness could be of concern to seabird species already under threat (Brooke, 1995).

Conversely, in many cases hybridisation can act adaptively, for example by introducing novel characteristics that boost survival or fitness in a population (Tompkins et al., 2006, Grant and Grant, 1992, Good et al., 2000). It has been shown in songbirds that hybrids may employ intermediate migratory strategies compared to parental forms (Delmore and Irwin, 2014). Whether this is adaptive or not depends largely on current and future environmental conditions. Although the Round Island population exists outside the original native ranges of its species the population appears to be growing.

The wide-ranging behaviour of tropical *Pterodroma* may help them to disperse and colonise new or extirpated islands, and the potential to thrive in new environments bodes well for their future, if the threat from invasive predators can be reduced.

The populations of petrels and other seabirds on Round Island are lucky, as it is one of the largest rodent-free tropical, high islands in the world (BirdLife International, 2016a). However the seabirds of the south-western Indian Ocean have no protection from human-induced threats at sea, with Marine Protected Areas (MPAs) covering less than 1% of the region (Le Corre et al., 2012). The south-western Indian Ocean supports high levels of other biodiversity, including charismatic and economically valuable species such as cetaceans, turtles and tuna, which are more challenging to track and monitor than seabird populations. Seabirds are easily caught, tagged and recovered at their breeding colonies and due to their position at the apex of most marine food chains they make good bioindicators of the health of marine ecosystems (Durant et al., 2009). Tracking seabirds at sea can locate areas of ecological importance not only for their own taxa but for other marine biodiversity also (Camphuysen et al., 2012, Lascelles et al., 2012, Ronconi et al., 2012). Knowledge of the breeding distribution of Round Island petrels may therefore be useful to conservation planning in the south-western Indian Ocean.

To map the distribution of petrels during their time at Round Island, I used light-based geolocators to track their at-sea movements. However, although geolocators are excellent for long-term tracking of seabirds and are cost-effective in terms of enabling a large sample of a population to be tracked, calculating locations from light data can be problematic when dealing with false daytime shading events. This shading noise was common in my data from colony-based petrels, as on their return to the island, they would sit on the leg-mounted tags and thus obscure the light sensor. In Chapter 3 I developed a new automated method to clean this shading noise from the data, where previously subjective and time consuming manual methods have been used.

Using this cleaned data, in Chapter 4 I described for the first time the distribution of colony-based Round Island petrels, highlighting the intra-population variation seen. This variation in the distribution of Round Island petrels is particularly relevant when considering the use of seabird distribution data in the identification of ecologically valuable areas. Seabird distributions have been shown to vary due to between-individual differences, for example sex (Ceia et al., 2012, Pinet et al., 2012b, Thiers et al., 2014, Quillfeldt et al., 2014, Weimerskirch et al., 2014), breeding stage (Pinet et al., 2012b, Cleeland et al., 2014, Weimerskirch et al., 1993), age (Péron, 2013, Thiers et al., 2014, Weimerskirch et al., 2014) and with an individual's personality (Patrick and

Weimerskirch, 2014). Environmental changes between years or seasons are also major influencers on seabird distribution (Deppe et al., 2014, Hennicke and Weimerskirch, 2014, Mendez et al., 2016, and Chapter 5). Assessing the degree of intra-population variability in distribution pattern is therefore important to ensure the provision of sufficient protection for behavioural diversity, which may safeguard seabird populations against future environmental change (Dias et al., 2013, Reed et al., 2010, Chirgwin et al., 2015). Despite this, hotspot approaches (Lascelles et al., 2012, Lascelles et al., 2016) do not currently represent the diversity of distribution patterns seen in wide-ranging species such as Procellariiformes. In Chapter 4 I demonstrated that accounting for intra-population variation in distribution patterns identified using a novel Bayesian Mixture Analysis increased the core distribution estimate by 47.8 - 79.6%, depending on the time-period considered. As animal trackers continue to get smaller and less expensive, allowing the tracking of more individuals, measuring intra-population variations similar to those of Round Island petrels will become more achievable. Whether MPAs can realistically hope to represent the diversity of behaviour found in some populations is questionable however. Larger MPAs may not necessarily be better conservation tools, as the larger the area protected, the more challenging and expensive it is to enforce regulations that support conservation goals (Agardy et al., 2011, Game et al., 2009). Nevertheless, Chapter 4 highlights the importance of considering intra-population variation when identifying distribution hotspots and describes for the first time the at-sea distribution of colony-based Round Island petrels, therefore providing insight into areas of ecological importance in the south-western Indian Ocean.

Due to their origins outside the Indian Ocean, the species of petrel found at Round Island provide a very unusual ‘common garden’ experiment in which different ancestral species (of different genotypes) can be observed experiencing the same environmental conditions. In Chapter 5 I explored both the influence of genotype on the distribution of Round Island petrels alongside environmental factors, as governed by the two main seasons of the south-western Indian Ocean. In contrast to recent findings on Macaronesian *Pterodroma* (Ramos et al., 2016), there was no evidence for spatial segregation between Round Island petrel species (*P. arminjoniana*, *P. neglecta* and *P. heraldica*). This has interesting implications for the taxonomic status of these species. Gene flow is often restricted between species or populations due to segregations in breeding and non-breeding habitat (Friesen, 2015, Friesen et al., 2007a), and if the species found at Round Island are not remaining segregated in this manner (as has

been demonstrated in Chapter 2), it may be that mixing between them becomes more common and species barriers may dissolve.

Although species assignment did not predict distribution patterns around Round Island, I found that the seasons did affect petrels at the colony. Specifically, the season (summer or winter) in which a petrel returned from migration influenced its distribution patterns in the first 60 days of its time at the colony, and in the last 60 days before it leaves on a subsequent non-breeding migration. This result suggests that the environmental conditions around the colony are influential throughout the colony-based season, and that petrels returning from migration are able to use information on conditions in their environment to change their distributions to target particular areas. This reactivity has been demonstrated in other seabirds (Warwick-Evans et al., 2016, Hennicke and Weimerskirch, 2014, Deppe et al., 2014, Mendez et al., 2016) and may be particularly advantageous to tropical seabird species to mitigate the patchy and unpredictable distribution of prey in tropical oceans (Weimerskirch, 2007, Ashmole, 1971). The findings of this chapter support a positive outlook for *Pterodroma*, as their adaptability to seasonally changing conditions allows them to thrive outside their native ocean, and therefore potentially resist changes in marine ecosystems caused by future climate change.

6.2. Future directions

The petrels of Round Island remain the only well documented example of a naturally occurring three-way hybrid in seabirds, however the research presented here suggests that inter-ocean migration and introgression between different species of *Pterodroma* may be more common than previously thought. This thesis demonstrates two ways of approaching the question of whether populations are mixing. From a tracking perspective, it is possible to show whether individuals are potentially coming into contact with non-natal colonies, and from a genetics perspective, it is possible to show whether populations are or have previously interbred.

Little research has been conducted on tropical *Pterodroma* breeding and non-breeding distributions. However, tracking data from Round Island petrels show that the population is very wide-ranging in the Indian Ocean during the non-breeding period, with individuals visiting all oceanic regions above $40^0$0'S, with the exception of the Somali Basin and the Mozambique Channel (Nicoll *et al. submitted*). In addition, preliminary tracking of immature Round Island petrels (<3 years old) suggest that young birds make long (~18 months), exploratory trips from their natal colony (Nicoll et

al., 2016), as has been demonstrated in other species (Péron, 2013, Weimerskirch et al., 2014). There is currently no tracking data published for the non-breeding periods of Trindade, Kermadec, Herald, Phoenix or Murphy's petrels in their native ranges (although there is breeding season tracking data for both Murphy's and Trindade petrels available on the 'Tracking Ocean Wanderers' dataset at http://www.seabirdtracking.org/). Tracking these species could help to inform our understanding of global gene flow in seabird populations. For example, in some cases differences in the level of gene flow between populations may be caused by patterns of at-sea dispersal during the non-breeding period (Burg and Croxall, 2001, Friesen et al., 2007a, Morris-Pocock et al., 2010, Friesen, 2015). This is especially well demonstrated in the Burg and Croxall (2001) study on the genus *Thalassarche*. This study showed that black-browed albatrosses (*T. melanophris* and *T. impavida*), which use different coastal shelf foraging areas, were genetically distinct between island populations, whereas the more oceanic, wider-ranging grey-headed albatrosses (*T. chrysostoma*) were globally panmictic. Wider-ranging species may be more likely to encounter individuals from other populations, while populations with restricted or distinct distributions are more likely to remain isolated, and therefore have lower migration rates (Friesen et al., 2007a, Morris-Pocock et al., 2010, Friesen, 2015). Future tracking studies on the non-breeding period of Atlantic Trindade petrels and Pacific species may reveal similarly dispersive distribution patterns, explaining the scale of gene flow in these species. In addition, it would be particularly interesting to track similar inter-ocean visits from petrels outside the Indian Ocean as seen in this thesis (Chapter 2). However, the challenge of tracking tropical *Pterodroma* outside the Indian Ocean lies in their inaccessibility, as often colonies are very remote and rarely visited by researchers. This poses problems for tagging sufficient sample sizes of individuals to study the variation in the distribution patterns of populations and to increase the chance of recording inter-ocean migrants, particularly when using affordable tags like geolocators, which must be recovered to acquire the recorded data.

Inaccessibility is also a barrier to obtaining greater numbers of genetic samples from current populations across the ranges of tropical *Pterodroma*. Sampling more individuals per species and colony would be particularly valuable to the study of widespread dispersal and gene flow, and may help to resolve some of the taxonomic confusion that prevails in the genus. As mentioned previously, insufficient sample sizes may have resulted in important connections between populations being missed in the past. Despite the challenges, I strongly recommend the collection of greater numbers of genetic samples from the ranges of the species studied in this thesis, particularly in

the Pacific Ocean. It was interesting that in Chapter 2 STRUCTURE analysis assigned Herald and Phoenix petrels to the same genetic cluster, since they closely resemble one another (Murphy and Pennoyer, 1952, Birdlife International, 2016b). A focused genetic study has not been applied to these two species, and therefore a study with a greater sample size and species-specific markers may help to resolve their similarities or differences. This could be important to the conservation status of the Phoenix petrel, which is currently classified as 'Endangered' (Birdlife International, 2016b).

In Chapter 2 I was able to classify 484 Round Island petrels into parental or hybrid species assignments using genotyping data. With these data, a number of new studies could be made on the Round Island population. Although in Chapter 5 I found no segregation in the spatial distribution of petrels of different genetic backgrounds, some seabird species are segregated from closely related species by allochrony (Ramos et al., 2016, i.e. temporal separation. Friesen et al., 2007b). Individual Round Island petrels are locked into an annual cycle that follows a roughly six-month migration followed by six months spent at the colony (presumably for a breeding attempt), but not all individuals arrive at the island at the same time of year. Now that a large number of individuals at Round Island have been genotyped, it would be interesting to investigate whether individuals assigned to different parental species had distinct breeding seasons at Round Island. Additionally, the breeding colony on Round Island is split into five sub-colonies across different locations on the island (Figure 1). It would be interesting to investigate whether these sub-colonies are segregated by genotype. Anecdotal reports suggest that Kermadec-type calls are more frequently heard at the sub-colony at the summit of Round Island (Figure 1, green points). It may be that this is the case because petrels tend to concentrate their flights around the summit of the island (M.A.C. Nicoll, *pers. com.*), however the potential for spatial segregation between species could now be tested using the data generated in this thesis. The temporal or spatial segregation of the petrel species found on Round Island may have demographic consequences for the population. For example, temporal segregation may lead to one parental species breeding during a time of year with advantageous environmental conditions, leading to an increase in breeding success for that sub-population group. Likewise, fitness differences may arise if one parental species out-competes others for superior nest sites, for example those sheltered from harsh weather conditions. Over time, fitness differences caused by temporal or spatial segregation may cause one or more species to dominate the Round Island population at the expense of other. Investigating these potential influences on the demography of

the Round Island population would therefore be a particularly relevant direction for future research.

6.3. Conclusion

To conclude, this thesis uses the unusual Round Island petrels as a model system to demonstrate that individual differences are important to consider when studying populations. Despite similarities in appearance, the Round Island population consists of individuals with very different ancestral backgrounds, and that this could be true of many other *Pterodroma* populations. This has yet to be studied at a larger scale and could have important conservation implications for threatened species, as many gadfly petrels are. Although differences in genotype do not influence colony-based distribution for the Round Island petrel, individuals within this population show considerable variation in their distributions around the colony, even during this demanding period of the annual cycle. Intra-population variation can be caused by a range of factors, and here I demonstrated that Round Island petrels are influenced by large-scale environmental conditions affected by seasonal change. Therefore, investigating individual differences is very important when gathering basic ecological knowledge of a population or species, as these differences not only offer insights into evolutionary processes, but help capture the natural variation in study populations, which is a vital step towards protecting biodiversity in the face of future change.

Appendix A

Additional material to accompany Chapter 2: Widespread gene flow between oceans in a pelagic seabird species complex.

Supplementary Methods

Monitoring and tracking of Round Island Petrels

Round Island petrels are ringed with numbered bands for individual recognition and monitored by the island's wardens, managed by the Mauritius Wildlife Foundation and the Mauritian Government National Parks and Conservation Service (Tatayah, 2010). Known nesting areas are visited once a month and petrels found during these visits are fitted with rings or are recorded as recaptures, and their breeding status is noted.

During monthly seabird monitoring surveys on Round Island between November 2009 and November 2012, 330 MK15 British Antarctic Survey geolocators (Cambridge, UK) were fitted onto adult petrels using plastic tarsal rings. Of these (220) were recovered, and due to high battery failure in the tags, only (116) contained useable data. The geolocators log light-levels, sea-surface temperature and immersion activity at 10 minute intervals (Fox and Phillips, 2010). The data were downloaded and decompressed using the software BAStrak (Fox and Phillips, 2010), which was also used to generate locations from light-level information. The start of petrel migration away from Round Island was determined by a visual inspection of light-level and activity data. Locations that fell over land masses were removed from the dataset and locations were mapped using ArcMap v10.2.2 (ESRI 2010).

Sample Collection

Blood samples were collected from unrelated adult petrels found at their nests during routine petrel surveying by the Mauritian Wildlife Foundation on Round Island. Petrels were sampled from across their five main nesting sites on the island. Blood was stored in absolute ethanol at room temperature in screw-topped rubber-sealed microfuge tubes and at a sample:ethanol ratio of 1:10 v/v (ca 50 μl of blood : 1.5 ml absolute ethanol). In addition to these samples, 176 Round Island petrel samples and 52 Trindade petrels were obtained from a previous study by Brown et al. (2010), which were also stored in absolute ethanol, as detailed above. Kermadec petrel blood

samples (N=41) from North Meyer Island (Kermadec Islands) were collected by Stefanie Ismar in 2008 and stored in Queen's Lysis Buffer (Seutin et al., 1991) and stored at room temperature.

Museum samples of Pacific species originated from skins collected during expeditions to the South Pacific islands in the 1910-30, which are held at the American Museum of Natural History. Tissue samples were taken from the footpad of the specimens using sterile scalpels and were stored at room temperature in a sterile screw-top Eppendorf microfuge tube.

DNA extraction

Genomic DNA was extracted from whole blood using an ammonium acetate precipitation method (Nicholls et al., 2000). All DNA extractions from museum footpad samples were carried out using a Qiagen DNeasy Blood & Tissue Kit (Qiagen, Manchester, UK). The protocol was based on the manufacturers instructions, however samples were incubated overnight at 56°C in a rotary incubator to increase protein digestion. Extraction of museum sample DNA was carried out at the Zoological Society of London, in a purpose built ancient-DNA lab, to avoid contamination with DNA from the contemporary blood samples extacted at the NERC Biomolecualr Analysis Facility (NBAF) at the University of Sheffield. The concentration of the DNA extracted from the blood and museum skin samples was estimated using a Nanodrop 8000 (Thermo Scientific, Denver, USA).

Loci development

Two di- and tetra-nucleotide repeat enriched genomic libraries were created from the blood samples of one *Pterodroma arminjoniana* individual from the Trindade and Martim Vaz archipelago and one *P. heraldica* individual from Mangareva in the Gambier Islands. The library was enriched according to the modifications of Armour et al. (1994) by Gibbs et al. (1997) for the following motifs (GT)n, (CT)n, (GTAA)n, (CTAA)n, (TTTC)n and (GATA)n. These were denatured and bound to magnetic beads following Glenn and Schable (2005). Following enrichment the dinucelotide- and tetranucleotide-enriched fragments were PCR amplified separately in parallel, three times each to obtain sufficient DNA (c5 µg) for next generation sequencing. Each 25µl PCR contained 2.0µl dinucleotide or tetranucleotide-enriched DNA, 1x reaction buffer (Bioline), 25µg/ml BSA, 150µM dNTPs, 0.5µM Sau-L-A linker/primer (Royle et

al., 1992), 2.0 mM MgCl2 and 1 unit of DNA Taq polymerase (Bioline) and were amplified as by Glenn and Schable (2005). The di- and tetra-nucleotide PCRs were pooled together and the resultant mixed enriched DNA was purified using a QIAquick PCR purification column (Qiagen) and eluted in 40µl to create a concentration of c125 ng/µl. DNA concentration was measured on the Nanodrop 8000 (Thermo Scientific). The pooled PCR amplified enriched fragments were 454-sequenced (Roche, FLX) at the NERC Biomolecular Analysis Facility at the University of Liverpool. PCR primer sets were designed for 42 *P. arminjoniana* (*Parm01* to *Parm42*) and 40 *P. heraldica* (*Phel01* to *Phel40*) unique sequences using PRIMER3 software (Rozen and Skaletsky, 2000). Each locus was initially amplified separately and multiplex sets were developed for the loci selected for further analysis.

In addition to the species specific primers developed in this study, the following loci were also shown to have cross species utility; *TG01-114*, *TG03-002*, *TG13-009*, *TG13-017*, *TG01-148*, *TG03-031* and *Tgu06* (Dawson et al., 2010) and *Calex01* (Küpper et al., 2007). Due to a stutter appearance on chromatograms a pigtail sequence of GTTTCTT was added to the 5' end of the reverse primers for *Parm05* and *Parm11* to reduce noise from variable adenylation during the PCR (Brownstein et al., 1996).

DNA amplification and genotyping

DNA was amplified using Qiagen Multiplex PCR kits. Each 2µl PCR reaction contained 1µl of Qiagen Multiplex PCR Master Mix, 0.2µM of each primer and approximately 10ng of air-dried template DNA (following Kenta et al., 2008). Samples were PCR amplified in four multiplex sets (MP) each containing between three and five fluorescently-labelled microsatellite DNA markers, and one sex typing marker (*Z-002A, Z-002B* or *Z-002D*, (Dawson et al., 2007) or *Z37B* (Dawson et al., 2015). MP1: *Phel15*, *Parm29*, *Parm22*, *Parm20* and *Z-002B*; MP2: *Parm31*, *Tgu06*, *Phel12*, *TG13-017*, *Calex01* and *Z-002A*; MP3: *TG03-002*, *Phel35*, *TG13-009*, *Parm34* and *Z37B*; MP4: *Phel33*, *Phel28*, *Phel30* and *Z-002D* (Table 4).

PCR amplification was performed using a touchdown PCR cycle as follows: 95°C for 15 min; then 9 cycles of 94°C for 30 sec, 65°C for 90 sec (reducing by 1°C per cycle), 72°C for 60 sec followed by 25 cycles of 94°C for 30 sec, 55°c for 90 sec, 72°C for 60 sec and then a final extension step of 30 min at 60°C. A fraction of this product was loaded onto an ABI 3730 DNA Analyser (Applied Biosystems) with GeneScan ROX-500 size standard and allele sizes were scored using GeneMapper v. 3.7 software (Applied Biosystems). In most cases, genotypes were accepted if the sample

produced the same genotype on three separate occasions, but where this was not possible, the output produced by GeneMapper was visually assessed and genotypes only accepted if the chromatograms showed strong peak morphology.

Calculation of genetic diversity

Genetic diversity was measured by calculating the number of alleles per locus, observed and expected heterozygosity (H_o and H_e), and allelic richness for each species (Trindade petrel, Herald petrel, Kermadec petrel, Murphy's petrel and Phoenix petrel) in its native range (Table 5). The number of alleles per locus, H_o and H_e were calculated in CERVUS, and allelic richness was calculated in FSTAT v.2.9.3 (Goudet et al., 2002). Since 3 of the 12 markers used were developed from Trindade petrel (*P. arminjoniana*) DNA, and 5 were developed from Herald petrel (*P. heraldica*) DNA, evidence for ascertainment bias (Ellegren et al., 1995) was tested by comparing observed heterozygosity and allelic richness in the eight species-specific markers between the different species. This was done using ANOVA in the programming environment R v.3.1.2. (R Development Core Team, 2013).

Marker testing

The null allele frequency of each locus was estimated using CERVUS v.3.0.7 (Kalinowski et al., 2007). The deviation of loci from Hardy-Weinberg equilibrium and linkage disequilibrium between groups of loci were calculated using GENEPOP (web v.4.2, Raymond and Rousset, 1995). A subset of 161 samples were randomly re-extracted and genotyped to assess the data for genotyping errors (allelic dropout and false alleles) using PEDANT (Johnson and Haydon, 2007). Errors were calculated per-genotype, as is conventional (Broquet and Petit, 2004). All museum samples were genotyped at least twice (up to four times, maximum), since not all alleles amplified in PCR for some samples. This increased the consistency of allele scoring, as DNA extracted from museum samples can be prone to degradation, leading to allelic dropout (Taberlet et al., 1996).

STRUCTURE Analysis

For the full dataset, 15 independent models were run for each number of specified clusters (K= 3–5), with 10^6 MCMC iterations, and a burn-in period of 10^4. Models were

run without any prior population information, and assuming admixture. The 10 models with the highest mean Ln likelihood for each value of *K* were chosen out of the total 15 using the online service STRUCTURE HARVESTER v0.6.94 (Earl, 2012). These models were then re-entered into STRUCTURE HARVESTER to identify the most likely value of *K* using *ΔK* values (Evanno et al., 2005). The output from STRUCTURE HARVESTER was then summarised using the software CLUMPP (Jakobsson and Rosenberg, 2007) and visualised using the software DISTRUCT (Rosenberg, 2004) (Figure 17). Preliminary STRUCTURE analyses and their model conditions, exploring a larger range of *K* values and the effect of removing markers out of Hardy-Weinberg equilibrium are described in Figure 18 and Figure 19.

Supplementary Results

All of the microsatellite loci used in the analyses were autosomal in all five petrel species (Trindade, Kermadec, Herald, Phoenix and Murphy's petrel) tested based on the presence of heterozygotes in known females and males for each species. Analysis of the suite of autosomal microsatellite markers separately within each species revealed that four out of the 16 loci had a high estimated null allele frequency (>0.2) in three of the five species (and these were therefore discarded from further analysis (*Parm20*, *Parm34*, *Phel30* and *TG13-017*). Of the remaining 12 markers, eight (*Parm34*, *Parm29*, *Parm22*, *Parm20*, *Calex01*, *TG13017*, *Phel12*, *Phel30*) had a Hardy-Weinberg equilibrium value of less than 0.05 (or it could not be calculated) for three or more out of the five species (Table 5). Further STRUCTURE analysis was conducted both with and without these eight markers (Figure 17 and Figure 18), as deviation from Hardy-Weinberg equilibrium can indicate migration, emigration and genetic structure between groups, which we did not want to mask. Out of 396 paired calculations of linkage disequilibrium between all loci in all six groups (five species and the mixed species population at Round Island), seven pairs of loci displayed linkage disequilibrium (LD, Table 6), five in the Round Island population, and two in Herald petrels. Since few pairs of loci displayed LD and no LD was detected in the other species groups (Trindade, Kermadec, Phoenix and Murphy's petrels), these loci were left in the dataset. Strong LD can lead to an overestimate of clustering in STRUCTURE analyses (Kaeuffer et al., 2007). However, STRUCTURE analysis was performed using different numbers of markers and the results were consistent between runs (Figure 17, Figure 18 and Figure 19), reflecting a genetic structuring that was logical given the species included in the analysis. Data from samples that failed to amplify for at least

75% (eight) of the remaining 12 markers were removed from further analyses, leaving a total sample size of 885 individuals (Table 1). Average allelic dropout per-genotype was 0.023 (S.E. = ±0.007) and the occurrence of false alleles in the dataset was estimated to be non-existent.

The observed heterozygosity and allelic richness in the eight species-specific markers did not differ significantly between the different species (H_O between species: $F_{4,28}$ = 0.47, P = 0.76; A_R between species: $F_{4,28}$ = 0.38, P = 0.82), although genetic diversity did differ between loci (H_O: $F_{7,28}$ = 11.48, P < 0.0001; A_R: $F_{7,28}$ = 17.97, P < 0.0001). This suggests that significant ascertainment bias was not present in the species-specific markers between the different species genotyped.

Supplementary Tables and Figures

Table 4: Details of the final 12 autosomal microsatellite loci used to genotype petrels in this study. All primers were used at a concentration of 0.2µM. T_m ^{0}C: Primer melting temperature.

Locus	Primer Sequence (5' - 3')	T_m ^{0}C	Multiplex set
Calex01	F: CTTCTCCATTGTTGTCACCTCCAGT R: GTTTCTTCTTGACTTGGCCTGAGGTTTAGGTT	F: 64.90 R: 64.90	MP2
Parm22	F: CAAGGTGACTGGCAAGAAATG R: GGGTTGAGGAGCAGTCTGTG	F: 60.67 R: 60.86	MP1
Parm29	F: AGTGCACTAGGAGCCTCACG R: AGCCCATGCTAGAACACAGC	F: 60.61 R: 60.43	MP1
Parm31	F: TCATGGATGCACGTAGGAAG R: AACGATTCTGATGCCTGGAC	F: 59.67 R: 60.08	MP2
Phel12	F: AAATAGCATCATGAACATACAGCAGTG R: GAAGCCGCTCGTCCTCAG	F: 62.61 R: 62.25	MP2
Phel15	F: TTCAGTTAAGACTCAAACTGCCTTC R: AAACAGGGAAGTGGCATCAG	F: 60.32 R: 60.11	MP1
Phel28	F: GCTTGGCTTAGTCTCGAGGTC R: TGTCTTATTTCAGCGATTAGTTTCAG	F: 60.53 R: 60.19	MP4
Phel33	F: GTGTTTGGAGGCTGGAGTTG R: TATGGATGCCACCCTACCAG	F: 60.69 R: 60.73	MP4
Phel35	F: AGTTAAGCCTGACTGAGCTAAAAC R: AAAAGCTATTGGAGTGAGTAAAGC	F: 57.62 R: 57.52	MP3
TG03-002	F: TCTTGCCTTTTTGGTATGAGTATAG R: TACAAAGCACTGTGGAGCAG	F: 58.09 R: 57.63	MP3
TG13-009	F: TGTGGTGGGATAGTGGACTG R: CTGTAAAATGTGCAAGTAACAGAGC	F: 59.39 R: 59.46	MP3
Tgu06	F: CGAGTAGCGTATTTGTAGCGA R: AGGAGCGGTGATTGTTCAGT	F: 58.30 R: 59.73	MP2

Table 5: Characteristics of the 12 microsatellite markers genotyped in each of the potential species found at Round Island. Each species group only includes individuals from the native range of the species, and not from the Round Island population. Size: allele size range, N_A: number of alleles, A_R: allele richness, H_O: observed heterozygosity, H_E: expected heterozygosity, HWE: P-value for Hardy-Weinberg test.

	All spp.		Trindade petrel					Herald petrel					Kermadec petrel				
Locus	**Size**	**N_A**	**N_A**	**A_R**	**H_O**	**H_E**	**HWE**	**N_A**	**A_R**	**H_O**	**H_E**	**HWE**	**N_A**	**A_R**	**H_O**	**H_E**	**HWE**
Calex01	229–244	8	2	2.00	0.35	0.40	0.02	3	2.20	0.15	0.17	0.06	5	2.64	0.12	0.13	0.02
Parm22	199–207	6	2	2.00	0.21	0.22	0.52	4	2.87	0.10	0.17	0.00	5	4.14	0.49	0.68	0.00
Parm29	130-–46	6	1	1.00	0.00	0.00	-	4	2.71	0.19	0.22	0.02	3	1.62	0.05	0.05	1.00
Parm31	91–107	10	2	1.95	0.13	0.19	0.06	3	2.81	0.21	0.26	0.01	7	3.65	0.29	0.30	0.13
Phel12	157–177	9	5	4.46	0.40	0.63	0.00	6	5.61	0.68	0.76	0.00	6	3.78	0.28	0.33	0.04
Phel15	86–90	3	1	1.00	0.00	0.00	-	2	1.37	0.03	0.03	1.00	3	2.66	0.22	0.22	0.87
Phel28	230–254	8	5	3.75	0.67	0.58	0.65	5	3.43	0.17	0.28	0.00	5	3.63	0.30	0.47	0.00
Phel33	116–164	13	9	7.85	0.81	0.84	0.59	10	7.89	0.83	0.86	0.01	11	8.14	0.71	0.74	0.01
Phel35	124–182	11	9	7.67	0.83	0.86	0.58	9	6.44	0.75	0.77	0.09	8	6.98	0.82	0.83	0.08
TG03-002	123–129	4	3	2.43	0.15	0.14	1.00	3	1.97	0.10	0.09	1.00	3	2.47	0.39	0.37	0.92
TG13-009	185–199	5	3	2.50	0.27	0.24	1.00	4	2.76	0.14	0.16	0.06	4	1.94	0.05	0.08	0.01
Tgu06	152–169	11	5	4.75	0.51	0.63	0.04	9	4.51	0.69	0.61	0.43	7	4.23	0.47	0.57	0.00
All loci (mean)		7.83	3.92	3.45	0.36	0.39	0.45	5.17	3.71	0.34	0.36	0.22	5.58	3.82	0.35	0.40	0.26

Table 5 continued.

	All spp.		Murphy's petrel					Phoenix petrel				
Locus	**Size**	**N_A**	**N_A**	**A_R**	**H_O**	**H_E**	**HWE**	**N_A**	**A_R**	**H_O**	**H_E**	**HWE**
Calex01	229–244	8	3	2.61	0.23	0.40	0.00	2	1.19	0.01	0.01	0.00
Parm22	199–207	6	3	3.00	0.00	0.61	0.00	2	1.43	0.03	0.03	1.00
Parm29	130-–46	6	3	2.69	0.21	0.20	1.00	6	4.39	0.53	0.57	0.04
Parm31	91–107	10	7	6.63	0.77	0.81	0.12	4	3.39	0.52	0.46	0.18
Phel12	157–177	9	6	4.38	0.50	0.64	0.00	7	5.65	0.79	0.78	0.89
Phel15	86–90	3	1	1.00	0.00	0.00	-	3	1.82	0.05	0.06	0.07
Phel28	230–254	8	4	3.57	0.54	0.63	0.06	3	2.65	0.19	0.22	0.05
Phel33	116–164	13	8	5.42	0.79	0.72	0.69	11	7.49	0.83	0.83	0.34
Phel35	124–182	11	8	7.41	0.88	0.84	0.02	8	5.93	0.76	0.76	0.09
TG03-002	123–129	4	3	2.27	0.29	0.30	0.70	4	3.01	0.28	0.25	1.00
TG13-009	185–199	5	3	1.91	0.07	0.07	1.00	3	2.26	0.10	0.12	0.01
Tgu06	152–169	11	7	4.87	0.70	0.66	0.84	5	3.74	0.45	0.53	0.25
All loci (mean)		7.83	4.67	3.81	0.41	0.49	0.40	4.83	3.58	0.38	0.39	0.33

Table 6: Populations and markers showing disequilibrium linkage using 'Genotypic linkage disequilibrium test' in GENEPOP version 4.2. Genotypic disequilibrium was tested for each pair of loci in each population using the log likelihood ratio statistic, with the default Markov chain parameters.

Population	Locus 1	Locus 2	P-Value	S.E.	Switches
Round Island	Parm22	Tgu06	0.0000	0.0000	4074
Round Island	TG03.002	Phel33	0.0000	0.0000	8817
Round Island	Tgu06	Phel33	0.0000	0.0000	2085
Round Island	Tgu06	Parm31	0.0018	0.0010	4821
Round Island	Phel15	Phel12	0.0041	0.0017	3709
Herald	Parm22	Phel15	0.0049	0.0023	9319
Herald	Tgu06	Phel12	0.0083	0.0035	2779

Table 7: Classification conditions for individual petrels based on estimated membership (*Q*) to one of four clusters identified using STRUCTURE analysis (Figure 17). Thresholds based on Vähä and Primmer (2006) and Marie et al. (2011).

Class	Description	Conditions
PureT	Trindade type	Trindade cluster *Q* >=0.9 OR *Q* for other clusters < 0.1
PureK	Kermadec type	Kermadec cluster *Q* >=0.9 OR *Q* for other clusters < 0.1
PureHP	Herald-Phoenix type	Herald-Phoenix cluster *Q* >=0.9 OR *Q* for other clusters < 0.1
PureM	Murphy's type	Murphy's cluster *Q* >=0.9 OR *Q* for other clusters < 0.1
TxK	Trindade and Kermadec hybrid	Trindade cluster *Q* >= 0.1 AND Kermadec cluster *Q* >= 0.1 AND *Q* for other clusters < 0.1
TxHP	Trindade and Herald-Phoenix hybrid	Trindade cluster *Q* >= 0.1 AND Herald-Phoenix cluster *Q* >= 0.1 AND *Q* for other clusters < 0.1
HPxK	Herald-Phoenix and Kermadec hybrid	Herald-Phoenix cluster *Q* >= 0.1 AND Kermadec cluster *Q* >= 0.1 AND *Q* for other clusters < 0.1
MxHP	Murphy's and Herald-Phoenix hybrid	Murphy's cluster *Q* >= 0.1 AND Herald-Phoenix cluster *Q* >= 0.1 AND *Q* for other clusters < 0.1
TxHPxK	Trindade, Herald-Phoenix and Kermadec hybrid	Trindade cluster *Q* >= 0.1 AND Herald-Phoenix cluster *Q* >= 0.1 AND Kermadec cluster *Q* >= 0.1 AND Murphy's cluster *Q* < 0.1

Table 8: Genetic differentiation between island populations of the study species and petrels found at Round Island. F_{ST} values (below the diagonal) were calculated in FSTAT, and P-values (above the diagonal) were obtained after 2100 permutations. F_{ST} values in bold are significant.

Species →		**Mixed**	**Trindade**	**Herald**			**Kermadec**			
↓	**Location →**	**Round Island**	**Trindade**	**Ducie**	**Marquesas**	**Oeno**	**Ducie**	**Juan**	**Kermadec**	**Rapa**
	↓									
Mixed	**Round Island**		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trindade	**Trindade**	**0.02**		0.00	0.00	0.00	0.00	0.00	0.00	0.00
Herald	**Ducie**	**0.07**	**0.13**		0.00	0.23	0.00	0.00	0.00	0.00
	Marquesas	**0.10**	**0.15**	**0.04**		0.00	0.00	0.00	0.00	0.00
	Oeno	**0.09**	**0.14**	0.01	**0.01**		0.00	0.00	0.00	0.00
Kermadec	**Ducie**	**0.13**	**0.17**	**0.20**	**0.24**	**0.20**		0.00	0.00	0.05
	Juan	**0.10**	**0.11**	**0.20**	**0.24**	**0.21**	**0.04**		0.00	0.04
	Kermadec	**0.08**	**0.10**	**0.15**	**0.19**	**0.17**	**0.05**	**0.02**		0.00
	Rapa	**0.07**	**0.11**	**0.13**	**0.17**	**0.14**	0.01	**0.02**	**0.02**	
Murphy's	**Marotiri**	**0.37**	**0.36**	**0.37**	**0.39**	**0.35**	**0.32**	**0.30**	**0.34**	**0.32**
	Oeno	**0.36**	**0.36**	**0.35**	**0.37**	**0.34**	**0.32**	**0.31**	**0.33**	**0.32**
Phoenix	**Christmas**	**0.12**	**0.17**	**0.03**	**0.06**	**0.03**	**0.23**	**0.24**	**0.18**	**0.17**
	Pitcairn	**0.07**	**0.12**	-0.01	**0.03**	0.01	**0.20**	**0.20**	**0.14**	**0.12**
	Marquesas	**0.12**	**0.17**	**0.05**	**0.06**	**0.04**	**0.23**	**0.24**	**0.18**	**0.18**
	Phoenix	**0.11**	**0.15**	**0.04**	**0.07**	**0.03**	**0.20**	**0.20**	**0.15**	**0.14**

Table 8 continued.

Species →		Murphy's		Phoenix			
↓	Location →	Marotiri	Oeno	Christmas	Pitcairn	Marquesas	Phoenix
	↓						
Mixed	Round Island	0.00	0.00	0.00	0.00	0.00	0.00
Trindade	Trindade	0.00	0.00	0.00	0.00	0.00	0.00
Herald	Ducie	0.00	0.00	0.00	0.56	0.00	0.00
	Marquesas	0.00	0.00	0.00	0.00	0.00	0.00
	Oeno	0.00	0.00	0.00	0.24	0.00	0.00
Kermadec	Ducie	0.00	0.00	0.00	0.00	0.00	0.00
	Juan	0.00	0.00	0.00	0.00	0.00	0.00
	Kermadec	0.00	0.00	0.00	0.00	0.00	0.00
	Rapa	0.00	0.00	0.00	0.00	0.00	0.00
Murphy's	Marotiri		0.00	0.00	0.00	0.00	0.00
	Oeno	**0.07**		0.00	0.00	0.00	0.00
Phoenix	Christmas	**0.36**	**0.35**		0.00	0.40	0.70
	Pitcairn	**0.37**	**0.36**	**0.03**		0.00	0.01
	Marquesas	**0.35**	**0.32**	0.00	**0.05**		0.25
	Phoenix	**0.32**	**0.30**	0.00	**0.04**	0.01	

Migration from…

Species →		**Mixed**	**Trindade**	**Herald**			**Kermadec**			
↓	**Location →**	**Round Island**	**Trindade**	**Ducie**	**Marquesas**	**Oeno**	**Ducie**	**Juan**	**Kermadec**	**Rapa**
	↓									
Mixed	**Round Island**	**0.7444 ± 0.030576**	**0.1828 ± 0.035672**	0.0012 ± 0.002352	**0.0137 ± 0.010192**	0.0007 ± 0.001372	0.0008 ± 0.001568	0.0007 ± 0.001372	**0.0482 ± 0.010388**	0.0044 ± 0.006468
Trindade	**Trindade**	0.0151 ± 0.026068	**0.9141 ± 0.04312**	0.006 ± 0.011368	0.0082 ± 0.015288	0.0057 ± 0.011172	0.0059 ± 0.011172	0.0058 ± 0.010976	0.0057 ± 0.010976	0.0089 ± 0.016464
Herald	**Ducie**	0.0092 ± 0.017836	0.0088 ± 0.017248	**0.7598 ± 0.053116**	**0.1328 ± 0.062132**	0.0078 ± 0.015092	0.0129 ± 0.021756	0.0078 ± 0.014896	0.0079 ± 0.015484	0.0089 ± 0.017444
	Marquesas	0.0119 ± 0.022148	0.0105 ± 0.019992	0.0312 ± 0.035084	**0.8466 ± 0.061544**	0.0093 ± 0.01764	0.0098 ± 0.01862	0.0094 ± 0.017836	0.0094 ± 0.018032	0.0093 ± 0.017836
	Oeno	0.0125 ± 0.022736	0.0104 ± 0.019404	**0.0803 ± 0.065464**	**0.1333 ± 0.073304**	**0.6774 ± 0.019992**	0.0095 ± 0.018032	0.0095 ± 0.018032	0.0094 ± 0.01764	0.0104 ± 0.019404
Kermadec	**Ducie**	0.0097 ± 0.018424	0.0088 ± 0.016856	0.0095 ± 0.018032	0.0091 ± 0.017248	0.0088 ± 0.01666	**0.8317 ± 0.055076**	0.0087 ± 0.01666	0.0089 ± 0.017052	**0.0698 ± 0.046452**
	Juan	0.011 ± 0.020188	0.0098 ± 0.018032	0.0083 ± 0.01568	0.0078 ± 0.015092	0.0077 ± 0.0147	**0.1758 ± 0.056644**	**0.6752 ± 0.016072**	0.0078 ± 0.0147	**0.0654 ± 0.048608**
	Kermadec	0.0104 ± 0.018424	0.0218 ± 0.02254	0.0048 ± 0.009408	0.0047 ± 0.009212	0.0049 ± 0.009212	0.0219 ± 0.02842	0.0049 ± 0.009016	**0.7164 ± 0.0294**	**0.191 ± 0.04802**
	Rapa	0.0122 ± 0.023128	0.0108 ± 0.020188	0.0111 ± 0.020776	0.0177 ± 0.028028	0.0079 ± 0.014896	**0.0579 ± 0.044884**	0.0081 ± 0.015484	0.0079 ± 0.015092	**0.8266 ± 0.059976**
Phoenix	**Christmas**	0.0093 ± 0.016856	0.0072 ± 0.013916	**0.0763 ± 0.05194**	0.0109 ± 0.020188	0.0074 ± 0.014112	0.0074 ± 0.014112	0.0075 ± 0.014504	0.0073 ± 0.01372	0.0081 ± 0.015288
	Pitcairn	0.0103 ± 0.019796	0.0105 ± 0.019992	**0.0627 ± 0.051156**	**0.132 ± 0.071344**	0.0104 ± 0.0196	0.0202 ± 0.026264	0.0102 ± 0.019404	0.0103 ± 0.019796	0.0115 ± 0.021756
	Marquesas	0.0103 ± 0.019208	0.0107 ± 0.020188	**0.0402 ± 0.039592**	0.0204 ± 0.035868	0.008 ± 0.014896	0.0083 ± 0.015876	0.0079 ± 0.015288	0.0079 ± 0.015092	0.0099 ± 0.01862
	Phoenix	0.011 ± 0.02058	0.0107 ± 0.020384	**0.0482 ± 0.046256**	0.0143 ± 0.026068	0.0107 ± 0.019992	0.0144 ± 0.025284	0.0108 ± 0.020188	0.0108 ± 0.020188	0.0114 ± 0.02156

Table 9: Results table from final BAYESASS analysis, including Round Island samples. Migration rates calculated are a proportion of the 'Migration to...' population (rows) that originate from the 'Migration from…' population (columns), per generation. Confidence intervals are 1.96 x the standard deviation, as described in (Rannala, 2012). Significant migration rates are highlighted in bold. Grey cells indicate the proportion of non-migrants per generation in each population.

Table 9 continued.

		Migration from…			
Species →		**Phoenix**			
↓	**Location →**	**Christmas**	**Pitcairn**	**Marquesas**	**Phoenix**
	↓				
Mixed	**Round Island**	0.0007 ± 0.001372	0.0007 ± 0.001372	0.0012 ± 0.002156	0.0007 ± 0.001372
Trindade	**Trindade**	0.0057 ± 0.010976	0.0058 ± 0.011172	0.0076 ± 0.014504	0.0057 ± 0.010976
Herald	**Ducie**	0.0079 ± 0.015288	0.0079 ± 0.015092	0.0204 ± 0.034104	0.008 ± 0.015484
	Marquesas	0.0094 ± 0.017836	0.0095 ± 0.018228	0.0242 ± 0.039004	0.0095 ± 0.018228
	Oeno	0.0092 ± 0.01764	0.0094 ± 0.017836	0.0194 ± 0.031556	0.0093 ± 0.01764
Kermadec	**Ducie**	0.0087 ± 0.01666	0.0087 ± 0.01666	0.0087 ± 0.016856	0.0088 ± 0.016856
	Juan	0.0077 ± 0.0147	0.0078 ± 0.0147	0.0077 ± 0.014896	0.0079 ± 0.014896
	Kermadec	0.0048 ± 0.009016	0.0048 ± 0.009016	0.0049 ± 0.009408	0.0048 ± 0.009212
	Rapa	0.0079 ± 0.015092	0.0081 ± 0.015484	0.0159 ± 0.02646	0.0079 ± 0.015092
Phoenix	**Christmas**	**0.6749 ± 0.015484**	0.0073 ± 0.013916	**0.1687 ± 0.057428**	0.0076 ± 0.014308
	Pitcairn	0.0104 ± 0.0196	**0.6787 ± 0.02254**	0.0226 ± 0.039788	0.0102 ± 0.019208
	Marquesas	0.0079 ± 0.015092	0.0081 ± 0.015288	**0.8526 ± 0.060368**	0.0079 ± 0.015092
	Phoenix	0.011 ± 0.020972	0.0108 ± 0.02058	**0.1567 ± 0.064288**	**0.6793 ± 0.023716**

Migration from…

Species →		Trindade	Herald			Kermadec			
↓	Location →	Trindade	Ducie	Marquesas	Oeno	Ducie	Juan	Kermadec	Rapa
	↓								
Trindade	**Trindade**	**0.9243 ± 0.039984**	0.0059 ± 0.011172	0.0059 ± 0.011368	0.0086 ± 0.015876	0.006 ± 0.011564	0.0059 ± 0.011368	0.0123 ± 0.021756	0.0059 ± 0.011564
Herald	**Ducie**	0.0078 ± 0.014896	**0.6753 ± 0.016464**	0.0079 ± 0.015092	**0.2341 ± 0.048608**	0.0082 ± 0.01568	0.0077 ± 0.0147	0.0079 ± 0.014896	0.0076 ± 0.0147
	Marquesas	0.0088 ± 0.016464	0.0087 ± 0.016464	**0.6764 ± 0.018228**	**0.2223 ± 0.054292**	0.0088 ± 0.017052	0.0088 ± 0.01666	0.0088 ± 0.016268	0.0089 ± 0.016856
	Oeno	0.0109 ± 0.020776	0.01 ± 0.018424	0.0103 ± 0.019012	**0.8639 ± 0.066444**	0.0101 ± 0.0196	0.01 ± 0.019404	0.0129 ± 0.023716	0.0101 ± 0.019208
Kermadec	**Ducie**	0.0089 ± 0.017052	0.009 ± 0.016856	0.0093 ± 0.017248	0.0095 ± 0.018032	**0.8398 ± 0.056644**	0.0091 ± 0.017444	**0.0695 ± 0.047628**	0.0089 ± 0.01666
	Juan	0.0091 ± 0.017444	0.0079 ± 0.015092	0.0081 ± 0.015288	0.0081 ± 0.01568	**0.1811 ± 0.057624**	**0.6754 ± 0.01666**	**0.0706 ± 0.051352**	0.0081 ± 0.015288
	Kermadec	0.0231 ± 0.027244	0.0052 ± 0.010192	0.005 ± 0.009604	0.0069 ± 0.013132	0.0181 ± 0.028224	0.0051 ± 0.009996	**0.9092 ± 0.046256**	0.0051 ± 0.0098
	Rapa	0.0093 ± 0.017248	0.0076 ± 0.014504	0.0077 ± 0.014896	0.0091 ± 0.017052	**0.0523 ± 0.039396**	0.0077 ± 0.0147	**0.2 ± 0.052332**	**0.6754 ± 0.016856**
Phoenix	**Christmas**	0.0087 ± 0.016856	0.0081 ± 0.015092	0.0079 ± 0.015092	0.0387 ± 0.061936	0.0131 ± 0.021952	0.0078 ± 0.014896	0.0091 ± 0.017444	0.008 ± 0.01568
	Pitcairn	0.0107 ± 0.020384	0.0103 ± 0.019208	0.0103 ± 0.019796	**0.1978 ± 0.062328**	0.0202 ± 0.02646	0.0103 ± 0.0196	0.0111 ± 0.020972	0.0102 ± 0.019404
	Marquesas	0.0075 ± 0.013916	0.0075 ± 0.014504	0.0076 ± 0.0147	0.0123 ± 0.022148	0.0077 ± 0.014504	0.0075 ± 0.014504	0.0077 ± 0.0147	0.0075 ± 0.014308
	Phoenix	0.0108 ± 0.02058	0.0109 ± 0.021168	0.0109 ± 0.020972	0.0212 ± 0.03626	0.0126 ± 0.02352	0.011 ± 0.020776	0.0111 ± 0.021168	0.011 ± 0.02058

Table 10: Results table from BAYESASS analysis, excluding Round Island samples. Otherwise, as described in Table 9.

Table 10 continued.

Species →		*Migration from…* Phoenix			
Migration to… ↓	Location → ↓	Christmas	Pitcairn	Marquesas	Phoenix
Trindade	**Trindade**	0.0076 ± 0.013916	0.0059 ± 0.011172	0.0059 ± 0.011172	0.0059 ± 0.011368
Herald	**Ducie**	0.0203 ± 0.02842	0.0078 ± 0.0147	0.0077 ± 0.014896	0.0078 ± 0.0147
	Marquesas	0.0222 ± 0.032144	0.0087 ± 0.016464	0.0088 ± 0.016856	0.0089 ± 0.016856
	Oeno	0.0317 ± 0.048608	0.01 ± 0.019012	0.0102 ± 0.019404	0.0101 ± 0.019208
Kermadec	**Ducie**	0.0092 ± 0.017444	0.0091 ± 0.017248	0.0088 ± 0.01666	0.009 ± 0.017052
	Juan	0.008 ± 0.015484	0.0079 ± 0.014896	0.0079 ± 0.014896	0.0079 ± 0.015092
	Kermadec	0.0068 ± 0.01274	0.0051 ± 0.0098	0.0052 ± 0.009996	0.0051 ± 0.0098
	Rapa	0.008 ± 0.015288	0.0075 ± 0.014504	0.0075 ± 0.014504	0.0077 ± 0.0147
Phoenix	**Christmas**	**0.8748 ± 0.071932**	0.0078 ± 0.0147	0.008 ± 0.015092	0.0079 ± 0.015092
	Pitcairn	0.0203 ± 0.035084	**0.6786 ± 0.022344**	0.0103 ± 0.019404	0.01 ± 0.019012
	Marquesas	**0.2446 ± 0.045864**	0.0077 ± 0.014504	**0.6751 ± 0.016072**	0.0074 ± 0.014112
	Phoenix	**0.1991 ± 0.064484**	0.0109 ± 0.02058	0.0109 ± 0.02058	**0.6795 ± 0.023716**

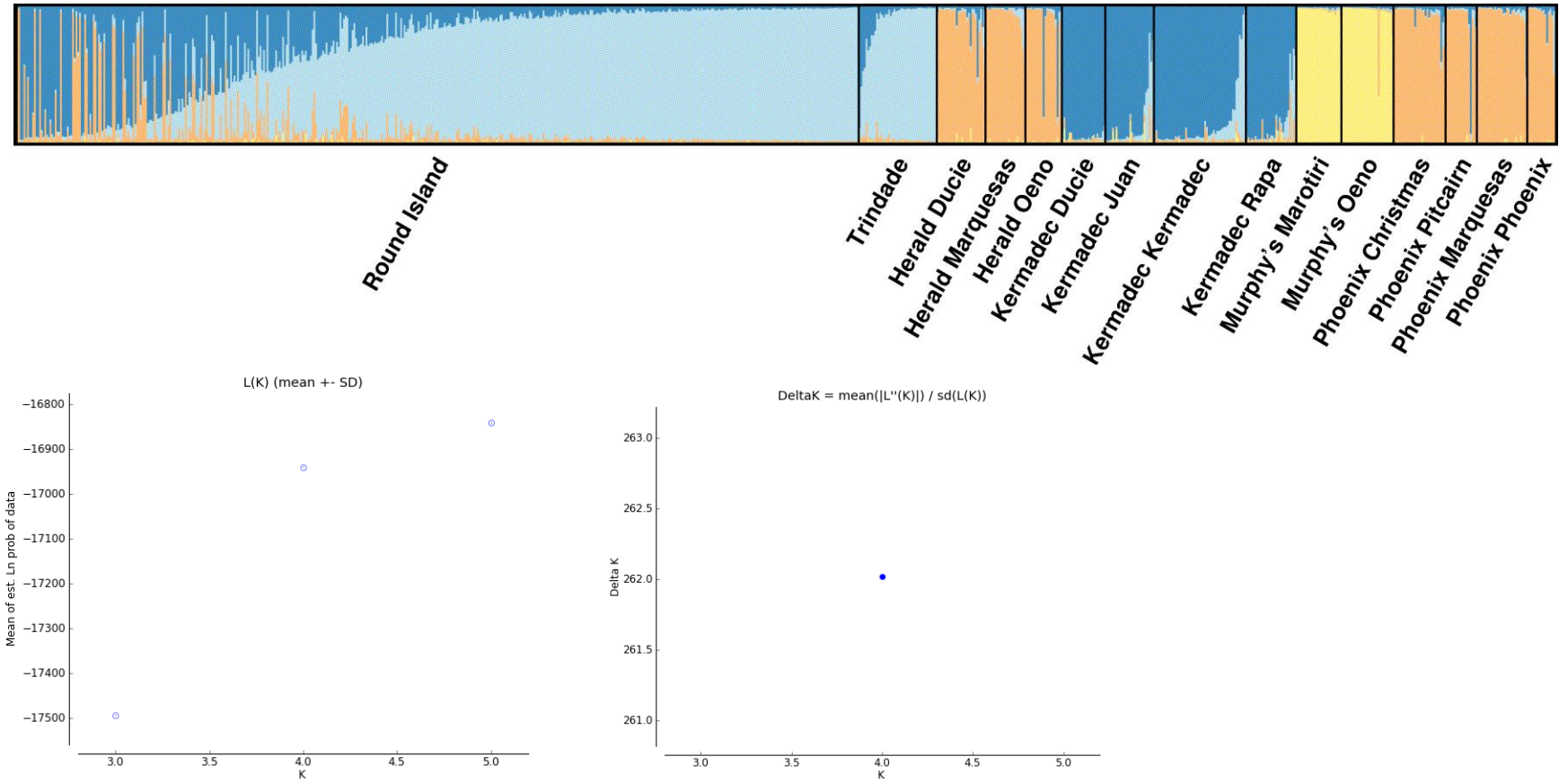

Figure 17: (Top) Plot showing final STRUCTURE analysis results, where *K* (number of clusters) equalled 4. Each bar represents a single individual and colours in each bar represent the proportion of times in 10^6 MCMC iterations that an individual was assigned to a particular cluster. Individuals are grouped by their species and island of origin (separated by black vertical lines), with the exception of Round Island, where species is unknown. The analysis did not include information population structure *a priori*. (Bottom right) Mean probability of different models of population structure (*K* = 3 – 5), from STRUCTURE HAVESTER. (Bottom left) The second order rate of change (Δ*K)* of the probability following (Evanno et al., 2005), from STRUCTURE HARVESTER.

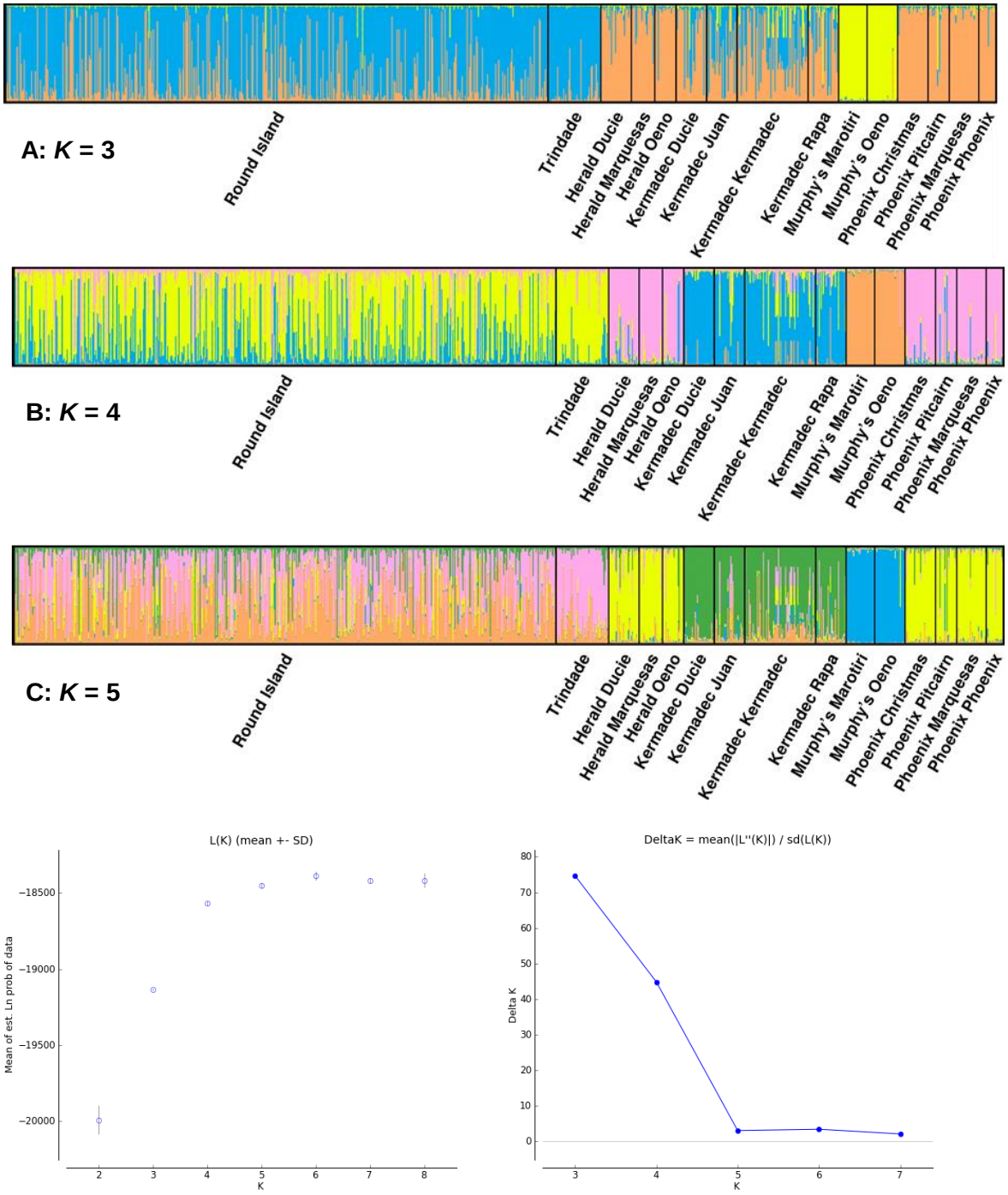

Figure 18: Plots showing STRUCTURE analysis results, where *K* (number of clusters) equalled 3 (A), 4 (B) or 5 (C). Using Δ*K* values, STRUCTURE HARVESTER suggested *K* of 3 or 4 as the most likely number of clusters. Four autosomal markers from the total 16 (*Parm34*, *Parm20*, *TG13-017* and *Phel30*) were removed from the dataset because they failed the null allele frequency test (they were not below 20% for over 60% of the species groups). Five independent models were run for each number of specified clusters (*K* = 2 – 8), with $5x10^4$ MCMC iterations, and a burn-in period of 10^4. Models were run without any prior population information, and assuming admixture. (Bottom right) Mean probability of different models of population structure (*K* = 2 – 8) ± standard deviation, from STRUCTURE HAVESTER. (Bottom left) The second order rate of change (Δ*K)* of the probability following (Evanno et al., 2005), from STRUCTURE HAVESTER.

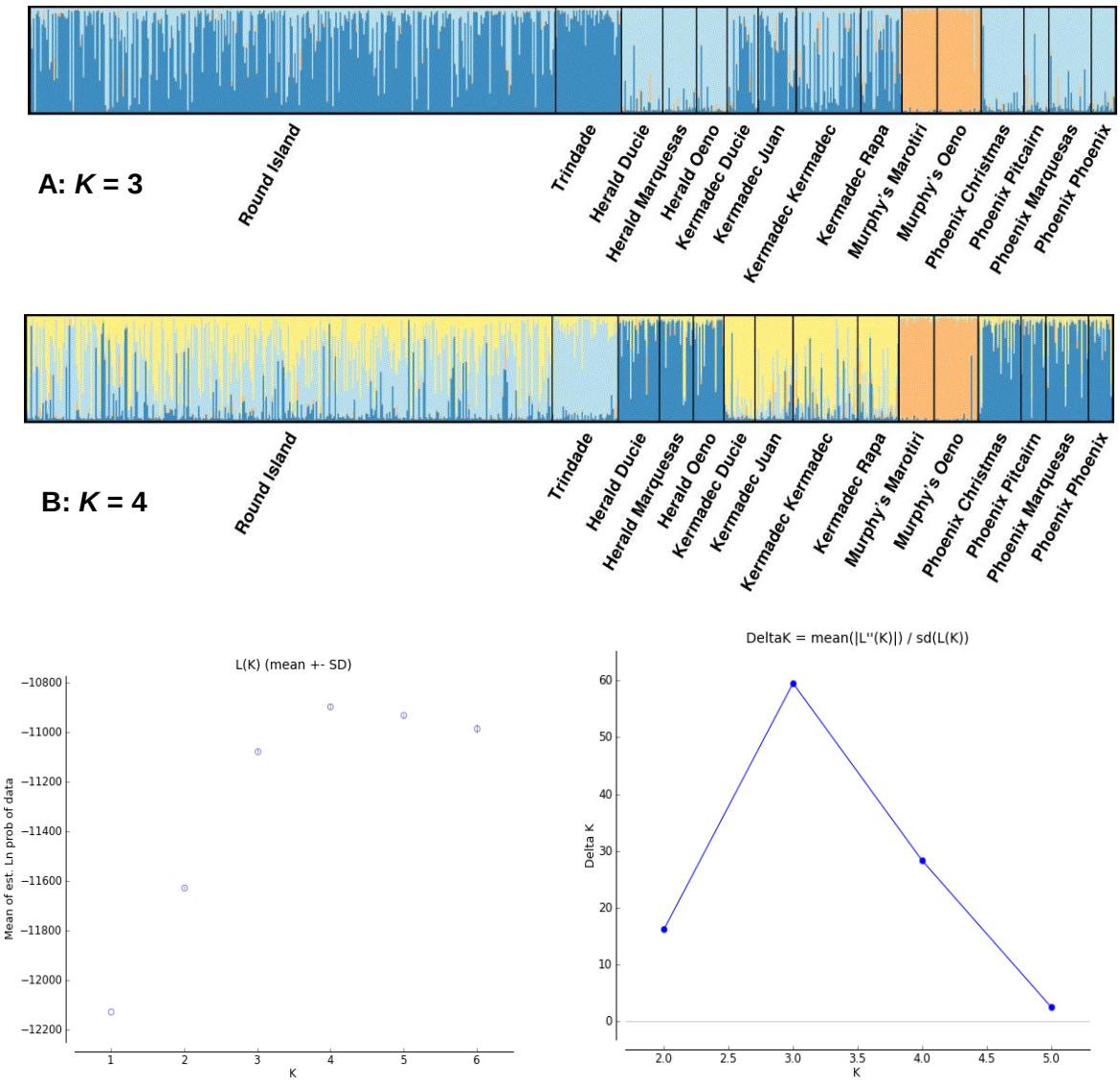

Figure 19: Plots showing STRUCTURE analysis results, where *K* equalled 3 – 4 (top to bottom). Using Δ*K* values, STRUCTURE HARVESTER suggested *K* = 3 was the most likely number of clusters. Eight autosomal markers from the total 16 (*Parm34*, *Parm29*, *Parm22*, *Parm20*, *Calex01*, *Phel12*, *TG13-017* and *Phel30*) were removed from the dataset because they failed the Hardy-Weinberg equilibrium test i.e. were not over 0.05 for more than 50% of the species groups. Ten independent models were run for each number of specified clusters (*K* = 1 – 6), with 10^5 MCMC iterations, and a burn-in period of 10^4. Models were run without any prior population information, and assuming admixture. (Bottom right) Mean probability of different models of population structure (*K* = 1 – 6) ± standard deviation, from STRUCTURE HAVESTER. (Bottom left) The second order rate of change (Δ*K)* of the probability following (Evanno et al., 2005), from STRUCTURE HAVESTER.

Appendix B

Data cleaning scripts used in Chapter 3: An approach for recovering degraded geolocation data in animal tracking studies.

CleanLight_link_script

```
#set the working directory
setwd("C:/CleanLight/Github/")

#Geolight is needed for remove_suspect_days:

# install.packages("GeoLight")
# install.packages("dygraphs")
# install.packages("xts")
library(GeoLight)
library(dygraphs)
library(xts)

#Call the 2 scripts used in the CleanLight method, these should
be stored in the working directory:

#1 clean_light - scans for interrupted light levels and
replaces.
#2 remove_suspect_days - iteratively remove days from the data
set that are unrealistically short given the previous day
length.

source("clean_light_v3.R")
source("remove_suspect_days_v3.R")

#name of the file…
inputfile<- "example.lig"

data.lig<-read.table(inputfile,
sep=',',col.names=c('check','sdate_time','','light'),stringsAsFa
ctors=FALSE)

# Construct an xts series:
```

```
dates <- strptime(data.lig$sdate_time, "%d/%m/%y %H:%M:%S", tz =
"GMT")
series <- xts(data.lig$light, order.by = dates, tz="GMT")

dygraph(series, main = "Uncleaned light data") %>%
  dySeries(c("V1"), label = "Light") %>%
  dyRangeSelector()

# npts = number of data points to include in the moving window.
# users should try a few on to see which works best for their
data.

npts<- 36

# Apply clean_light and save to that file:
cleaned.lig = clean_light(data.lig, npts)
colnames(cleaned.lig) <- c('check','sdate_time','','light')

# Construct an xts series:
dates <- strptime(cleaned.lig[, 2], "%d/%m/%y %H:%M:%S", tz =
"GMT")
cleaned.series <- xts(cleaned.lig[, 4], order.by = dates,
tz="GMT")

dygraph(cleaned.series, main = "Cleaned light data") %>%
  dySeries(c("V1"), label = "Light") %>%
  dyRangeSelector()

# Create a filename for the light file with clean_light applied:

clean_light_outputfile = output_filename=gsub(".lig",
"_npts36.lig", inputfile)

# Output dataframe to file with no colnames and no rownames:
write.table(cleaned.lig,file=clean_light_outputfile,sep=',',
col.names=FALSE,row.names=FALSE, quote=FALSE)

# Apply suspect days and save to that file:
final.lig <- remove_suspect_days(cleaned.lig)
```

```
# Create a filename for the final file with suspect days
removed:
final_outputfile = gsub(".lig", "_clean.lig", inputfile)
write.table(final.lig, file=final_outputfile,
sep=',',col.names=FALSE, row.names=FALSE, quote=FALSE)


# Construct an xts series:
dates <- strptime(final.lig[, 2], "%d/%m/%y %H:%M:%S", tz =
"GMT")
final.series <- xts(final.lig[, 4], order.by = dates, tz="GMT")


# Plot final cleaned and removed series:
dygraph(final.series, main = "Final cleaned data") %>%
  dySeries(c("V1"), label = "Light") %>%
  dyRangeSelector()


# Try plotting all three series, offset to facilitate
visualisation...
dygraph(merge(series+200, cleaned.series+100, final.series),
main = "Final", group = "cleanLight") %>%
  dyRangeSelector()
```

clean_light script

```
# clean_light function (inputfile, npts):
clean_light <- function(data.lig, npts) {

  # Get times as text:
  time<-data.lig$sdate_time

  # Convert to 'R' times:
  time.lig<-strptime(data.lig$sdate_time,'%d/%m/%y %H:%M:%S')

  # Get light data:
  light<-data.lig$light

# Calculate 1-difference in light data, appending NA to end to
force vector to be same length.
# Calculates changes of light measurement between one time and
the next:
  d <- c(diff(light), NA)

  # Set maximum light threshold:
  f<-3
  max_light_thresh = npts/f

  # Create a vector of unknown values the same length as
'light':
  nlight <- NA*numeric(length(light))

  # For each light value...
  for (i in 1:length(light)) {

    is_currently_na = is.na(d[i]) #set NAs to NA

    is_diff_currently_positive = d[i]>0 #assign positive
differences in light to "is_diff_currently_positive"
    is_diff_currently_negative = d[i]<0 #assign negative
differences in light to "is_diff_currently_negative"

    if (i <= npts | i > (length(light)-npts)){
```

```
# If too near the beginning or end of the light data (within the
window 'npts'), set result to be NA:
      nlight[i]<-NA


    } else {


# Count numbers of negative differences in npts before point i
and assign to "n_negative_diff_in_window",
# Count numbers of positive differences in npts before point i
and assign to "n_positive_diff_in_window":


      n_negative_diff_in_window <- length(which(d[(i-
npts):i]<0))
      n_positive_diff_in_window <- length(which(d[(i-
npts):i]>0))


# Count the number of maximum light recordings (64) within i
plus and minus the width of npts:


      n_max_light_values_in_big_window = length(which(light[(i-
npts):(i+npts)]==64))


# If i isn't NA, and if the difference in light at i is
positive, and the number of negative differences in npts is
greater than zero,
# and the number of maximum light recordings in the time period
around i is less than the maximum light threshold,
# make i = 0 in nlight:


      if (!is_currently_na && is_diff_currently_positive &&
n_negative_diff_in_window > 0 &&
n_max_light_values_in_big_window < max_light_thresh) {


        nlight[i]<-0


# Else,
# if i isn't NA, and if the difference in light at i is
negative, and the number of positive differences in npts is
greater than zero,
# and the number of maximum light recordings in the time period
around i is less than the maximum light threshold,
# make i = 0 in nlight:
```

```
      } else if (!is_currently_na && is_diff_currently_negative
&& n_positive_diff_in_window > 0 &&
n_max_light_values_in_big_window < max_light_thresh) {


        nlight[i]<-0


# Else,

# if i isn't NA, and if the difference in light at i is
positive, and the number of negative differences in npts is
greater than zero,

# make i = 64 in nlight:


      } else if (!is_currently_na && is_diff_currently_positive
&& n_negative_diff_in_window > 0) {


        nlight[i] <- 64

# Else,

# if i isn't NA, and if the difference in light at i is
positive, and the number of negative differences in npts is
greater than zero,

# make i = 64 in nlight:


      } else {


# Else,

# if none of the above are true, make i in nlight the same as i
in light:


        nlight[i]<-light[i]

      }

    }

  }


n <- nlight # make n the same as nlight


# If n = 64 or 0, make those values 100:

n[n==64 | n==0] <- 100


# If n isn't 100 or is NA, make those values 0:
```

```
n[n!=100 | is.na(n)] <- 0

# If n is 100, make that value 1:
n[n==100] <- 1

 # Create yt_setones function needed later
 # Determine the rises and falls (sunrises and sunsets within x)

  yt_setones<-function(x){

      # If x is na, make 0:
      x[is.na(x)]<-0

      # Make an object called ends, in which the difference
      between x and 0 is less than 0 (sunset):
      ends<-which(diff(c(x,0))<0)

      # Make an object called starts, in which the difference
      between 0 and x is greater than 0 (sunrise):
      starts<-which(diff(c(0,x))>0)

    return(cbind(starts,ends)) # Return starts and ends combined
  }
# Calculate start and end of intermediate transitions (in
cleaned light data):
  r<-yt_setones(n)

# Calculate length of these transitions (or light period
length):
  r<-r[,2]-r[,1]+1

# If there are light periods that are shorter than the window…
  if (length(which(r<npts))>0){

# Construct matrix with light data as first column, then matrix
of unknowns the same length as light, the width of the window:
    outlight<-cbind(nlight,matrix(NA,length(light),npts))

# For each column in that unknown matrix (or for each point in
the window)…
```

```
    for (j in 1:npts){


# Calculate rolling difference of the 'j'th column of that
matrix:
      d<-c(diff(outlight[,j]),NA)


      # For each row…
      for (i in 1:dim(outlight)[1]){


      # If i in the rolling difference is NA, assign to
      'is_currently_na':
        is_currently_na = is.na(d[i])


      # If i in the rolling difference is positive, assign to
      'is_diff_currently_positive':
        is_diff_currently_positive = d[i]>0


      # If i in the rolling difference is negative, assign to
      'is_diff_currently_negative':
        is_diff_currently_negative = d[i]<0


# If i is less than or equal to npts, or if i is greater than
the number of rows of outlight minus npts…
        if (i<=npts | i>dim(outlight)[1]-npts){


# If too near the beginning and end (within the window) do
nothing.


        } else {
# Make 'n_negative_diff_in_window' a number the length of which
the difference between i minus npts and i is less than 0:


          n_negative_diff_in_window <- length(which(d[(i-
npts):i]<0))


# Make 'n_positive_diff_in_window' a number the length of which
the difference between i minus npts and i is greater than 0:


          n_positive_diff_in_window <- length(which(d[(i-
npts):i]>0))
```

```
# Make ‘n_max_light_values_in_big_window’ equal to the length of
which i rows in outlight plus or minus npts, in column j, equals
64:

          n_max_light_values_in_big_window =
length(which(outlight[(i-npts):(i+npts), j]==64))


# If i is not NA, and is positive, and the number of negative
differences in the window around i is greater than 0,

# and the number of maximum light values in the big window is
less than the maximum light threshold…


          if (!is_currently_na && is_diff_currently_positive &&
n_negative_diff_in_window > 0 &&
n_max_light_values_in_big_window < max_light_thresh) {


# set the value of this row in the next column to be 0:

            outlight[i,j+1]<-0


# If i is not NA, and is negative, and the number of positive
differences in the window around i is greater than 0,

# and the number of maximum light values in the big window is
less than the maximum light threshold…


          } else if (!is_currently_na &&
is_diff_currently_negative && n_positive_diff_in_window > 0 &&
n_max_light_values_in_big_window < max_light_thresh) {


# set the value of this row in the next column to be 0:

            outlight[i,j+1]<-0


# If i is not NA, and is positive, and the number of negative
differences in the window around i is greater than 0…


          } else if (!is_currently_na &&
is_diff_currently_positive && n_negative_diff_in_window > 0) {


# set the value of this row in the next column to be 64:

            outlight[i,j+1]<-64


          } else {
```

```
# If none of the above apply, set the value of this row in the
next column to be the value of this row:
            outlight[i,j+1]<-outlight[i,j]
          }
        }
      }
    }
    nlight<-outlight[,ncol(outlight)]
  }

  # Set those values that are NA to be 0:

  nlight[is.na(nlight)]<-0

  # Create output data frame:

  outmat<-data.frame(data.lig$check, data.lig$sdate_time,
data.lig$X, nlight)

  return(outmat)
}
```

remove_suspect_days script

```
# Requires plyr package
# Install.packages(plyr)
library(plyr)

# Get_suspect_days_all_geolight function:
# Calculates the mean and sd of daylight differences in 'data'
to create a threshold difference.
# Returns differences in the dataset that exceed this difference

get_suspect_days_all_geolight <- function(data) {

  if (nrow(data) > 15) {
    # Get mean difference in day lengths:
    mean_day_diff <- mean(data$DayDiff[!is.na(data$DayDiff)])
    # Get sd of difference in day lengths:
    sd_day_diff <- sd(data$DayDiff[!is.na(data$DayDiff)])

    # Calculate threshold as mean + 1*sd:
    threshold = mean_day_diff + sd_day_diff

# What dates exceed the mean+standard deviation difference in
daylength?

    result = list(data$tFirst[data$DayDiff > threshold])

    # Return resulting list:
    return(result)

  } else {
    cat("Error! Too few days") # If not more than 15 days.
    return(NULL)
  }
}

# remove_days_geolight function:
```

```
# Make a dataset called 'cleaned_data' from the date-times in
'data' that are not found in 'days':


remove_days_geolight <- function(data, days) {


  # When days are not NA…
  days = days[!is.na(days)]
  # Deleting days…
  # Make cleaned_data the date-times in days that are not in
data$tFirst
  cleaned_data <- data[!(strptime(data$tFirst,'%Y-%m-%d
%H:%M:%S') %in% strptime(days,'%Y-%m-%d %H:%M:%S')), ]


  # Order clean_data by $tFirst:
  cleaned_data <- cleaned_data[order(cleaned_data$tFirst), ]


  # Return cleaned_data:
  return (cleaned_data)
}


# remove_suspect_days function:


remove_suspect_days <- function(data.lig, max_day_diff=100) {


  # Set colnames explicity in case they are not set:
  colnames(data.lig) <- c('check','sdate_time','','light')
  datetime = strptime(data.lig$sdate_time, '%d/%m/%y %H:%M:%S')


  # Make datetime POSIXct:
  datetime <- as.POSIXct(datetime)


  # Use GeoLight twilightCalc function to calculate twilights
from light data:
  twilights <- twilightCalc(datetime,data.lig$light,
LightThreshold=10,preSelection=TRUE,maxLight=10,ask=FALSE,nsee=5
00)


  # Calculate day lengths by subtracting tFirst (sunrise time)
from $tSecond (sunset time) in minutes:
```

```
  twilights$DL = difftime(twilights$tSecond, twilights$tFirst,
units = "mins")


  # Remove very long day lengths:


  twilights = twilights[twilights$DL < 5000, ]


  # Make a column called DayDiff in twilights filled with zeros:


  twilights$DayDiff = 0


  # Subtract the sunrise time of each day from the following day
to get a difference in timing of sunrises:


  twilights$DayDiff[twilights$type==1] =
c(diff(twilights$DL[twilights$type==1]), NA)


  # Subtract the sunset time of each day from the following day
to get a difference in timing of sunsets:


  twilights$DayDiff[twilights$type==2] =
c(diff(twilights$DL[twilights$type==2]), NA)


  # Work only with transitions of type 1 (sunrises):
  cleaned_data = twilights[twilights$type == 1, ]


  too_few = FALSE


  # Iteratively detect and remove suspect days until the max
positive daylength difference is < 100 as defined by
max_day_length_diff above


  while (max(cleaned_data$DayDiff[!is.na(cleaned_data$DayDiff)])
> max_day_diff) {


    # Return suspect days, where day length differences exceed
the mean + standard deviation threshold:


    suspect_days <- get_suspect_days_all_geolight(cleaned_data)


    # If suspect_days is not null…
```

```
    if (!is.null(suspect_days)) {

      # Remove suspect days from the cleaned_data dataset, and
store as cleaned_days:

      cleaned_days <- remove_days_geolight(cleaned_data,
suspect_days[[1]])

      # Calculate difference in day length:

      cleaned_days$DayDiff = c(diff(cleaned_days$DL), NA)

      # Make cleaned_data equal cleaned_days:

      cleaned_data = cleaned_days
    }
  }

  # If there's no days left to clean, suspect_days will be NULL
  if (is.null(suspect_days)) too_few = TRUE

  # Make keep_days from the days left in the cleaned_data
dataset

  keep_days = strftime(cleaned_data$tFirst, '%Y-%m-%d')

  # Make orig_days from the days in the light dataset:

  orig_days = strftime(strptime(data.lig$sdate_time, '%d/%m/%y
%H:%M:%S'), '%Y-%m-%d')

  # Make rows_to_keep only include rows in the light data that
are present in cleaned_data

  rows_to_keep = which(orig_days %in% keep_days)

  # Remove rows that are not in rows_to_keep from the light data
and called clean_data
```

```
  clean_data = data.lig[rows_to_keep, ]
  return(clean_data)
}
```

Appendix C

Additional material to accompany Chapter 4: The importance of quantifying within-population variation in the at-sea distribution of colony-based seabirds when identifying marine hotspots.

Supplementary Methods

Deployment of geolocators

Geolocators were mounted onto 1mm or 0.75mm thick Salbex rings (industrial PVC, Sallu Plastics, UK) and attached to the petrels on their tarsi. Petrels were caught and tagged during seabird monitoring by the warden team on Round Island, operated by the Mauritian Wildlife Foundation (MWF) and the Mauritian Nation Parks and Conservation Service (NPCS). Petrels were either resting on the island or present with a chick or other petrels. Adults found incubating eggs were not tagged, to avoid disturbing incubation.

Generating locations

Daytime shading noise was created in the geolocation light data recorded by the geolocators when petrels resting on the island covered the light sensors on the tags. To counter the effect of this, a semi-automated data cleaning process was used to reconstruct clean light data during minor day time shading events from the colony-associated light data, and remove days where shading was too severe to confidently recover the light data. The cleaning process retains transitions between night and day in the light file, while unusual light level measurements, in the context of the data in the surrounding window, are replaced with either the maximum light measurement, 64 or a darkness measurement, zero (Fox and Phillips, 2010). Details of this process can be found in Chapter 3.

Bayesian Mixtures Analysis (BMA)

The grouping of individuals into similarly distributed mixtures requires a decision by the user on how to divide the overall distribution space of the population. Dividing the ocean into regions based on bathymetry (Figure 20) made ecological sense in this

study, as seabird foraging distributions are have been found to be influenced by bathymetry (Hyrenbach et al., 2002, Suryan et al., 2006, Navarro and Gonzlez-Solis, 2009b, Pinet et al., 2011a, Deppe et al., 2014, Young et al., 2015), as this plays a part in determining prey availability. Locations of individual petrels were counted in each ocean region using the *countpntsinpolys* tool in the software Geospatial Modelling Environment ('GME', Spatial Ecology, Beyer, 2012a) for the first 60 and/or (depending on whether an individual had both) last 60 days before/after a migration. These counts per region per individual were then analysed using the BMA, which calculated the optimal number of groups, known as 'mixtures', which represent the variability in counts between individuals. It then assigned individuals to these mixtures, based on similarities between petrels in the same mixtures, and differences from petrels in other mixtures. The outcome of this was that petrels of similar distribution in space between defined ocean regions were grouped together, and those with dissimilar distributions were grouped apart.

Mapping

Kernel density estimations were generated using a plate carrée projection, cell size 10km and search radius of 180km in ArcMap v10.2.2 (ESRI 2010). Isopleth contour lines representing the core 50% density of each petrel group and corresponding polygons were created using the *isopleth* function in GME. The area in km^2 was calculated using the *Calculate Geometry* tool in ArcMap for all the core (50% density) polygons. Core area polygons were joined using the *Merge* and *Dissolve* tool in ArcMap. The core areas of each of the colony-based periods were combined to create a polygon that encompassed the area covered by all three. The area of this polygon that was not included within the core area of all locations was calculated as a percentage. Similarly, the core areas of mixtures within colony-based periods were combined and the total areas were compared to the core area of the period from which they were derived.

Supplementary Results

Timing of petrel presence at Round Island

Peak petrel presence at the breeding colony occurs between October and November (Tatayah, 2010), and the deployment of geolocators was scheduled to take advantage

of this. Despite the timing of the deployment of the geolocators onto petrels at Round Island, the first return dates (start date of the tracked time period, Figure 21) of petrels with a full colony-based period of distribution data was spread throughout the year, with July having the most frequent number of petrels returning to the island (N=7, 30.4%). The start dates of the petrels' tracked during their early period at Round Island were spread similarly throughout the year, with peak numbers starting in July and August (N= 26, 30.5% each). The most frequently observed start of the petrels' late colony-based period occurred later in the year, as would be expected, with a modal month of November (N=22, 31.0%). However the numbers of petrels in their late period remained high in December (N=8, 11.3%) and January (N=14, 19.7%).

Supplementary Figures to Chapter 4

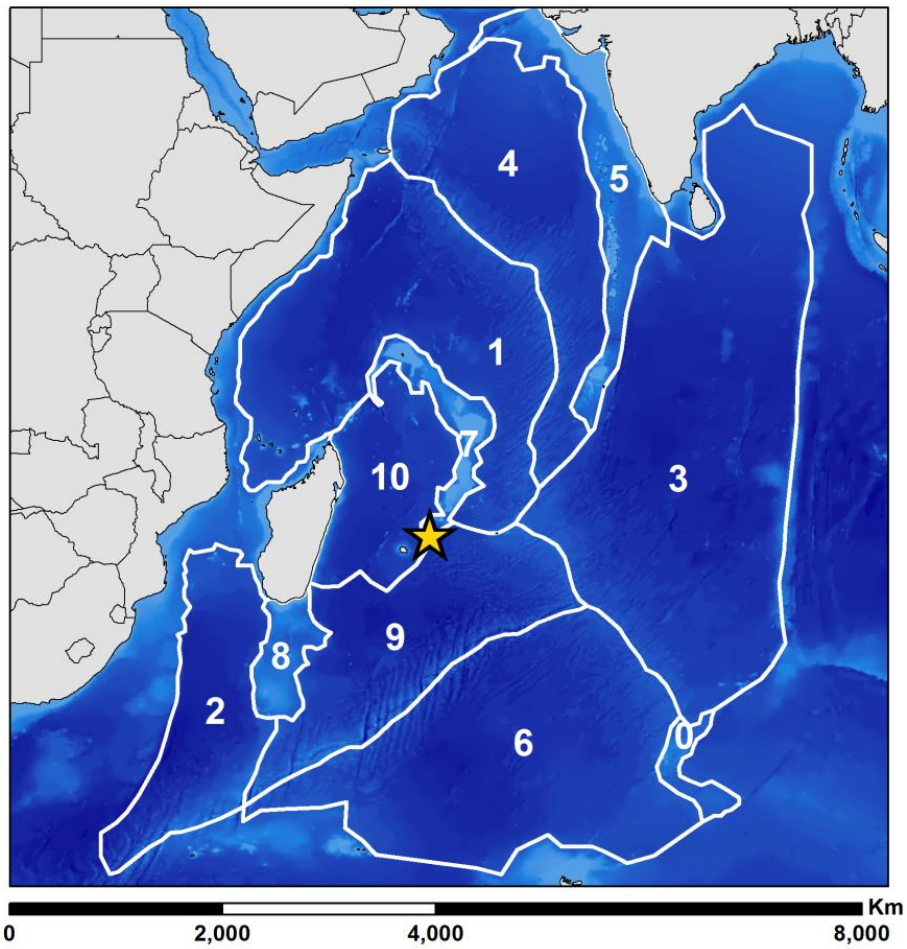

Figure 20: Division of Indian Ocean based on bathymetry features (basins and ridges). Petrel locations in each of the numbered regions were counted and this data was used in the BMA. (0) South-East Indian Ridge, (1) Somali Basin, (2) Mozambique Basin, (3) Mid-Indian Basin, (4) Arabian Basin, (5) Chagos-Laccadive Plateau, (6) Crozet Basin, (7) Mascarene Plateau, (8) Madagascar Plateau, (9) Madagascar Basin, (10) Mascarene Basin. The location of Round Island is indicated by the yellow star.

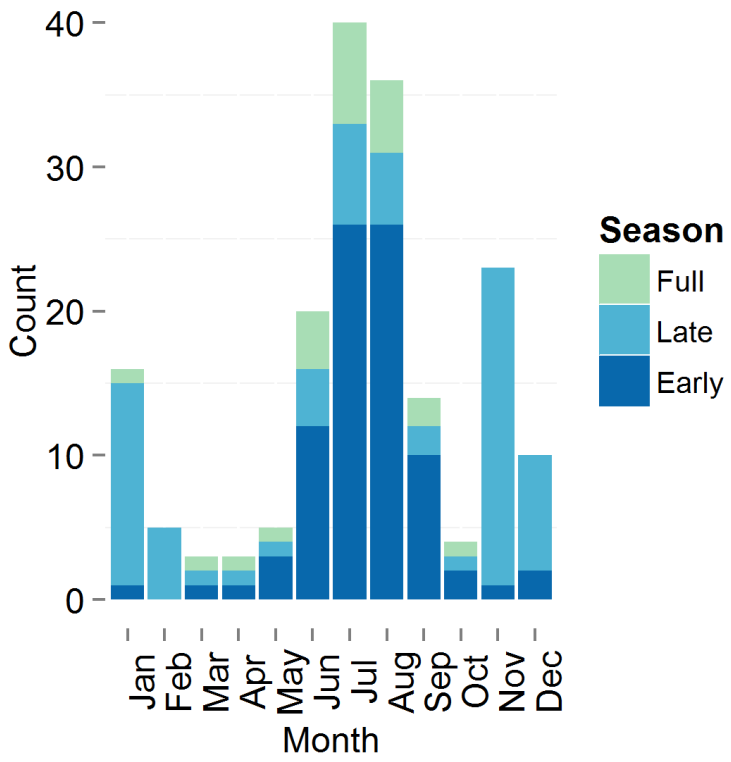

Figure 21: Histogram of the start dates of tracked periods for individuals in the full colony-based period (green), early period (dark blue) and late period (light blue).

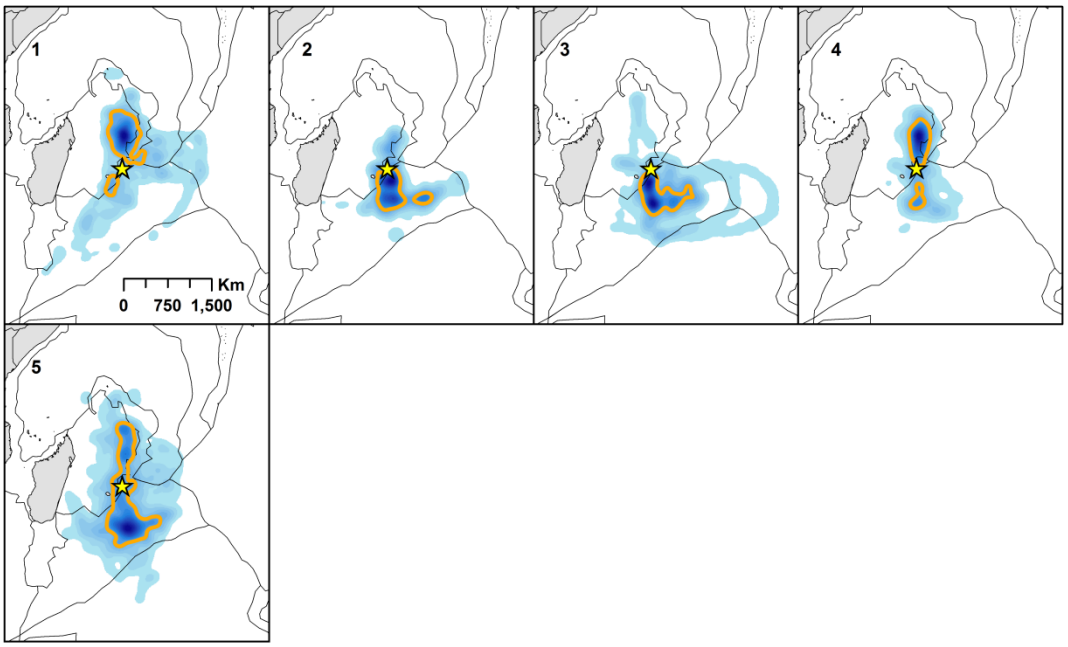

Figure 22: Kernel density maps for the 5 mixtures identified by the BMA in the full colony-based period. The 95% range estimates are represented in blue. The orange isopleth line shows the 50% density boundary, indicating the core foraging distribution area in each time period. Numbers of individuals per mixture: 1 (N=3), 2 (N=3), 3 (N=3), 4 (N=5), 6 (N=9).

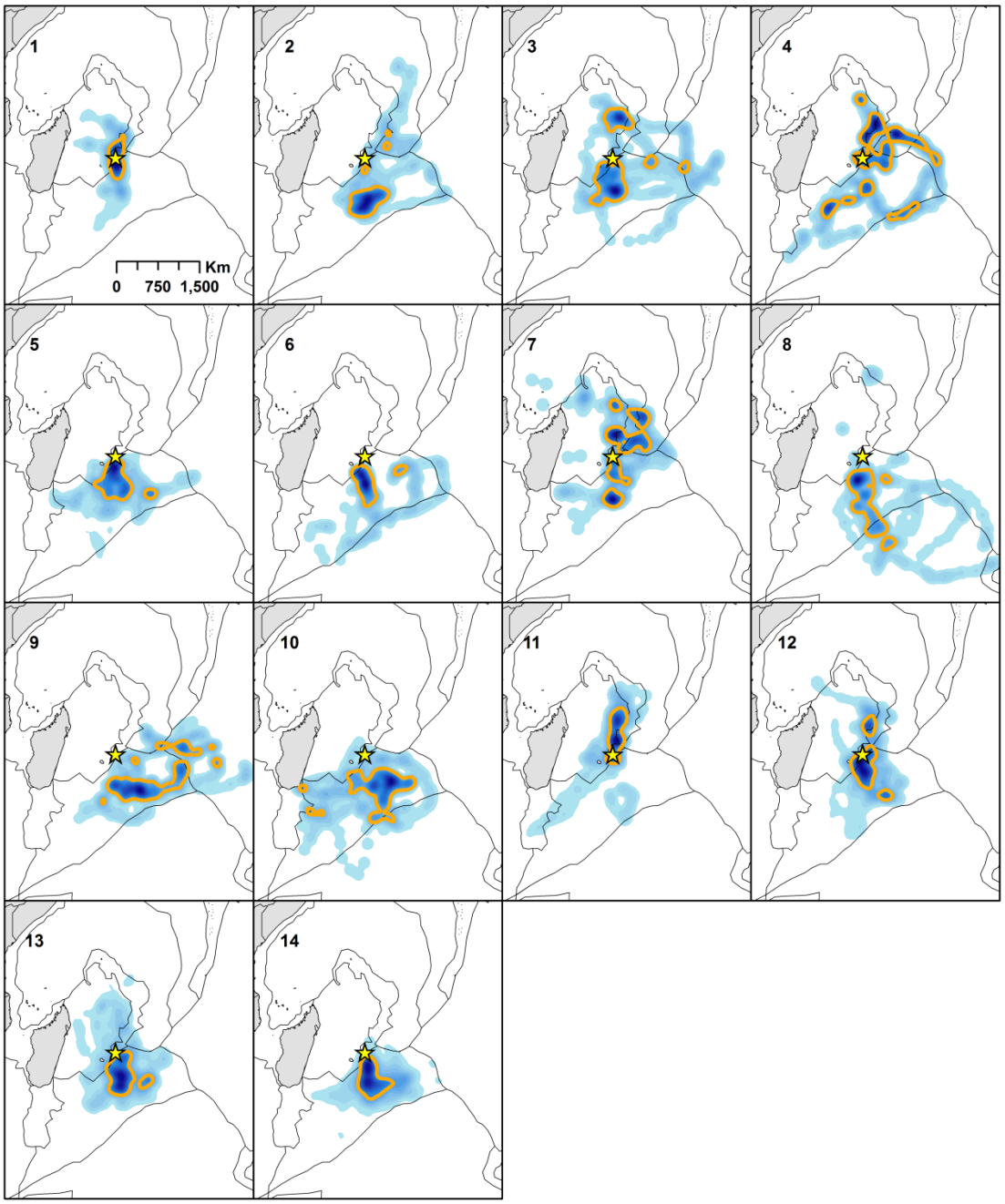

Figure 23: Kernel density maps for the 14 mixtures in the early colony-based period. The 95% range estimates are represented in blue. The orange isopleth line shows the 50% density boundary, indicating the core foraging distribution area in each time period. Numbers of individuals per mixture: 1 (N=3), 2 (N=4), 3 (N=3), 4 (N=2), 5 (N=5), 6 (N=2), 7 (N=4), 8 (N=3), 9 (N=3), 10 (N=4), 11 (N=4), 12 (N=7), 13 (N=10), 14 (N=31).

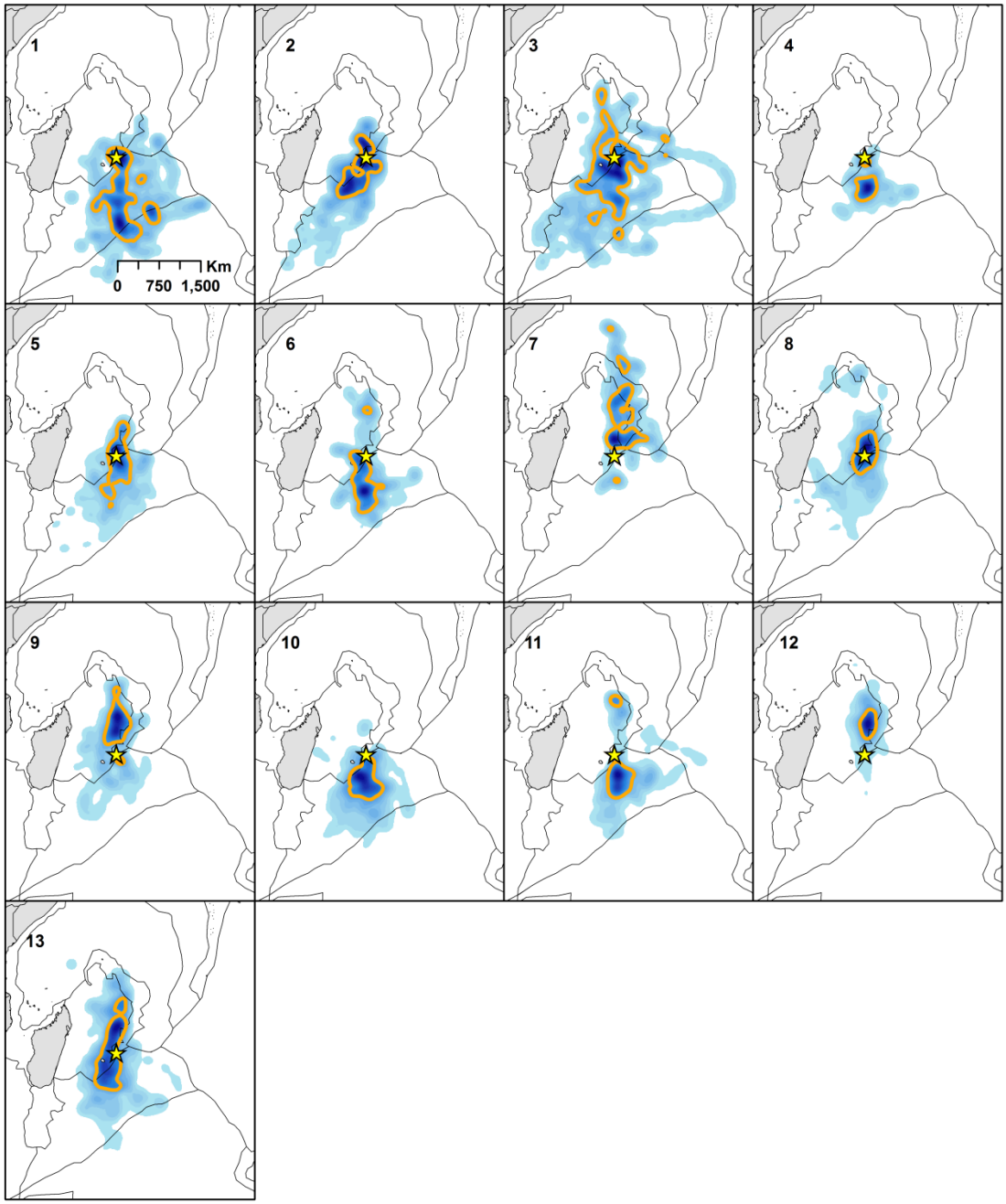

Figure 24: Kernel density maps for the 13 mixtures in the late colony-based period. The 95% range estimates are represented in blue. The orange isopleth line shows the 50% density boundary, indicating the core foraging distribution area in each time period. Numbers of individuals per mixture: 1 (N=4), 2 (N=4), 3 (N=5), 4 (N=3), 5 (N=5), 6 (N=4), 7 (N=3), 8 (N=8), 9 (N=5), 10 (N=7), 11 (N=7), 12 (N=8), 13 (N=8).

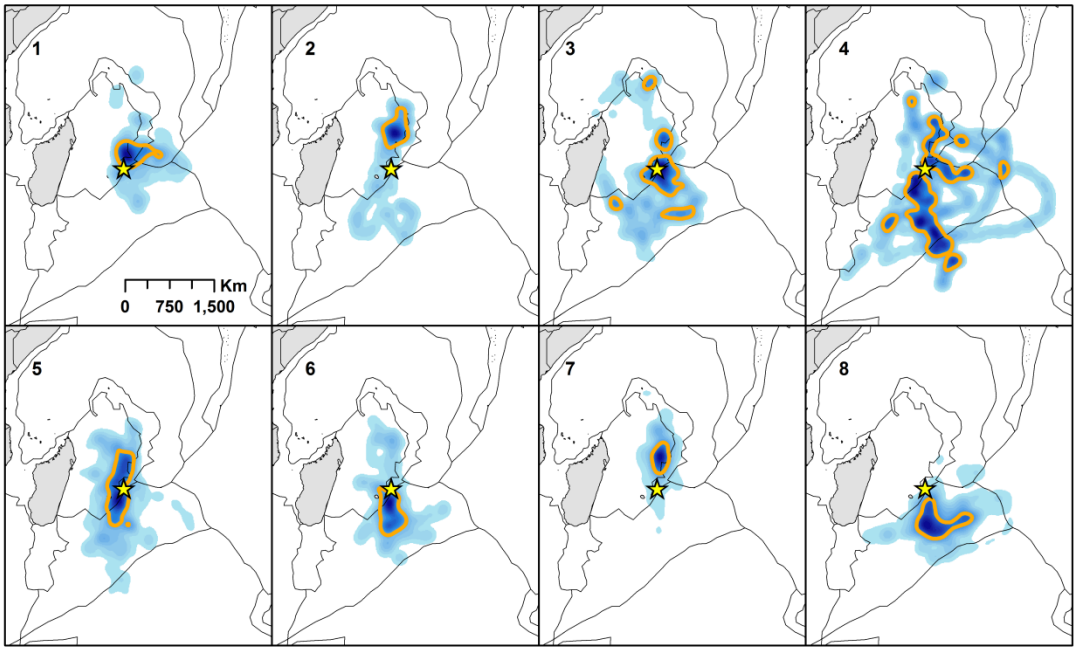

Figure 25: Kernel density maps for 8 mixtures found between individuals at different stages of the colony-based period. The early and late distributions for individuals were not assigned to the same mixtures in any case. The 95% range estimates are represented in blue. The orange isopleth line shows the 50% density boundary, indicating the core foraging distribution area in each time period. Numbers of individuals per mixture: 1 (N=3), 2 (N=2), 3 (N=5), 4 (N=4), 5 (N=5), 6 (N=6), 7 (N=7), 8 (N=14).

Appendix D

Additional material to accompany Chapter 5: Colony-based distribution of tropical petrels influenced by seasonal climate, but not genotype.

Supplementary Tables and Figures

Table 11: Numbers of petrels in each mixture category in the early and late colony-based periods. N_G = Number of genotyped petrels, N_T = Total number of petrels. For details on the assignment of original distribution mixtures using the Bayesian Mixture Analysis, see Chapter 4.

	3-level Distribution Mixture	**N_G**	**N_T**	**Original Distribution Mixture**	**N_G**	**N_T**
Early	SO	39	54	2	2	2
				5	2	4
				6	2	2
				8	2	3
				9	2	3
				10	4	4
				13	7	10
				14	18	26
	NO	4	4	11	4	4
	NS	16	18	1	3	3
				3	3	3
				4	1	2
				7	2	3
				12	7	7
				Total	59	76
Late	SO	14	18	4	1	3
				6	3	4
				10	6	6
				11	4	5
	NO	14	15	7	2	2
				9	5	5
				12	7	8
	NS	22	32	1	2	3
				2	2	3
				3	4	5
				5	5	5
				8	5	8
				13	4	8
				Total	50	65

Table 12: Coefficients (standard errors) from the top multinomial logistic regression model for the early colony-based period: Model 2.1, Table 3. Coefficients are shown for the influence of season on the two distribution categories (North Only and North and South) compared to the base category (South Only).

Distribution Category	Intercept	Summer
North Only	-11.12 (36.05)	11.81 (36.05)
North and South	-1.18 (0.29)	1.18 (1.04)

Table 13: Relative risk ratios from the top multinomial logistic regression model for the early colony-based period: Model 2.1, Table 3. Risk ratios are estimated against the baseline distribution category, South Only.

Distribution Category	Intercept	Summer
North Only	0.00	135089.30
North and South	0.31	3.25

Table 14: Coefficients (standard errors) from the top multinomial logistic regression model for the late colony-based period: Model 4.1 ,Table 3. Coefficients are shown for the influence of inter-annual seasons on the two distribution categories (North Only and North and South) compared to the base category (South Only).

Distribution Category	Intercept	Summer 2009	Winter 2010	Summer 2010	Winter 2011	Summer 2011
North Only	-0.41 (0.91)	-0.69 (1.22)	0.70 (1.19)	-15.78 (1333.28)	13.11 (233.73)	16.95 (0.00)
North and South	1.39 (0.65)	-1.39 (0.87)	-0.40 (0.94)	-2.08 (0.96)	10.62 (233.73)	-9.22 (0.00)

Table 15: Relative risk ratios from the top multinomial logistic regression model for the late colony-based period: Model 4.1, Table 3. Risk ratios are estimated against the baseline distribution category, South Only.

Distribution Category	Intercept	Summer 2009	Winter 2010	Summer 2010	Winter 2011	Summer 2011
North Only	0.67	0.50	2.00	0.00	492418.93	22903740.00
North and South	4.00	0.25	0.67	0.13	40997.73	0.00

Table 16: Predictions from the top multinomial logistic regression model for the early colony-based period: Model 2.1, Table 3. N = the number of individuals in each season of the dataset to which the model was fitted. Sub-totals of the number of individuals in each group of the dataset are shown in brackets.

Season	South Only	North Only	North/South	N
Winter	0.76 (52)	0 (0)	0.24 (16)	68
Summer	0.25 (2)	0.5 (4)	0.25 (2)	8

Table 17: Predictions from the top multinomial logistic regression model for the late colony-based period: Model 4.1, Table 3. N = number of individuals in each season from the dataset on which the model was fitted. Sub-totals of the number of individuals in each group of the dataset are shown in brackets.

Season-year	South Only	North Only	North/South	N
W_09	0.18 (3)	0.12 (2)	0.71 (12)	17
S_09	0.43 (6)	0.14 (2)	0.43 (6)	14
W_10	0.20 (3)	0.27 (4)	0.53 (8)	15
S_10	0.67 (6)	0.00 (0)	0.33 (3)	9
W_11	0.00 (0)	0.67 (6)	0.33 (3)	9
S_11	0.00 (0)	1.00 (1)	0.00 (0)	1

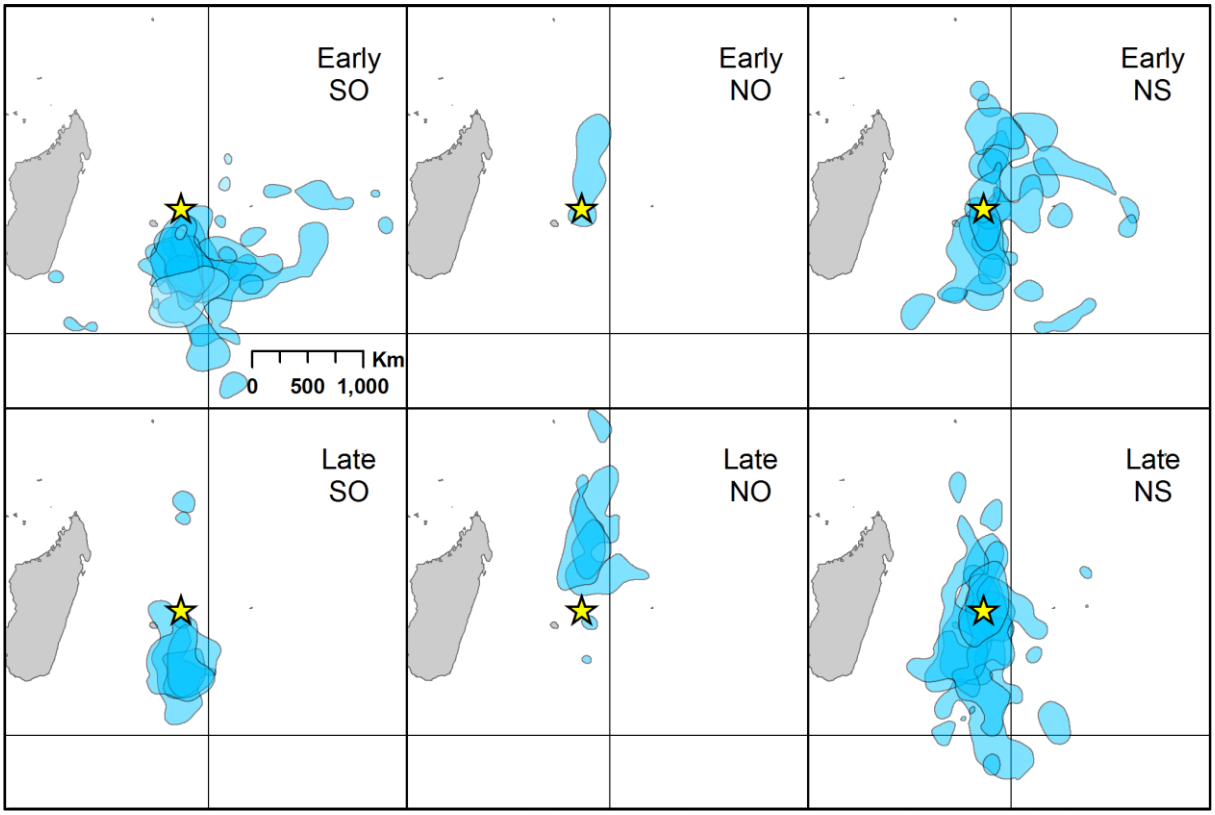

Figure 26: Core distributions (50% kernel density polygons, translucent blue) of mixtures from the early (top) and late (bottom) colony-based periods of all individual petrels in the study. ‘South Only’ (SO) distributions are predominantly focused to the south of Round Island (star), ‘North Only’ (NO) are predominantly to the north, and ‘North-South’ distributions do not have a strong presence in one over the other.

References

BirdLife International (2015) Species factsheet: Pterodroma heraldica. Downloaded from http://www.birdlife.org on 08/09/2015. [Online]. [Accessed].

ABBOTT, C. L. & DOUBLE, M. C. 2003. Genetic structure, conservation genetics and evidence of speciation by range expansion in shy and white-capped albatrosses. *Molecular Ecology,* 12**,** 2953-2962.

AGARDY, T., DI SCIARA, G. N. & CHRISTIE, P. 2011. Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Marine Policy,* 35**,** 226-232.

AINLEY, D. G., SPEAR, L. B., TYNAN, C. T., BARTH, J. A., PIERCE, S. D., GLENN FORD, R. & COWLES, T. J. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep Sea Research Part II: Topical Studies in Oceanography,* 52**,** 123-143.

ALLENDORF, F. W., LEARY, R. F., SPRUELL, P. & WENBURG, J. K. 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution,* 16**,** 613-622.

ANDERSON, O. R. J., SMALL, C. J., CROXALL, J. P., DUNN, E. K., SULLIVAN, B. J., YATES, O. & BLACK, A. 2011. Global seabird bycatch in longline fisheries. *Endangered Species Research,* 14**,** 91-106.

ANDO, H., KANEKO, S., SUZUKI, H., HORIKOSHI, K., CHIBA, H. & ISAGI, Y. 2011. Lack of genetic differentiation among subpopulations of the black-footed albatross on the Bonin Islands. *Journal of Zoology,* 283**,** 28-36.

ARCOS, J. M., BÉCARES, J., VILLERO, D., BROTONS, L., RODRÍGUEZ, B. & RUIZ, A. 2012. Assessing the location and stability of foraging hotspots for pelagic seabirds: An approach to identify marine Important Bird Areas (IBAs) in Spain. *Biological Conservation,* 156**,** 30-42.

ARMOUR, J. A. L., NEUMANN, R., GOBERT, S. & JEFFREYS, A. J. 1994. Isolation of human simple repeat loci by hybridization selection. *Human Molecular Genetics,* 3**,** 599-605.

ASHMOLE, N. 1971. Seabird ecology and the marine environment. In 'Avian Biology. Vol. 1'.(Eds DS Farner and JR King.) pp. 223–286. Academic Press: New York.

ASHMOLE, N. P. 1963. THE REGULATION OF NUMBERS OF TROPICAL OCEANIC BIRDS. *Ibis,* 103b**,** 458-473.

AUSTIN, J. J., WHITE, R. W. & OVENDEN, J. R. 1994. Population-genetic structure of a philopatric, colonially nesting seabird, the Short-tailed Shearwater (*Puffinus tenuirostris*). *The Auk***,** 70-79.

AVISE, J. C., NELSON, W. S., BOWEN, B. W. & WALKER, D. 2000. Phylogeography of colonially nesting seabirds, with special reference to global matrilineal patterns in the sooty tern (*Sterna fuscata*). *Molecular Ecology,* 9**,** 1783-1792.

BAIRLEIN, F., NORRIS, D. R., NAGEL, R., BULTE, M., VOIGT, C. C., FOX, J. W., HUSSELL, D. J. T. & SCHMALJOHANN, H. 2012. Cross-hemisphere migration of a 25 g songbird. *Biology Letters,* 8**,** 505-507.

BALLANCE, L. & PITMAN, R. S34. 4: Foraging ecology of tropical seabirds. Proc. 22 Int. Ornithol. Congr., Durban, 1999. 2057-2071.

BEERLI, P. 2009. How to use MIGRATE or why are Markov chain Monte Carlo programs difficult to use. *Population genetics for animal conservation,* 17**,** 42-79.

BEERLI, P. & FELSENSTEIN, J. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences,* 98**,** 4563-4568.

BEYER, H. L. 2012a. Geospatial modelling environment. *Spatial Ecology.[Online.] Available at www. spatialecology. com/gme.* Version 0.7.3.0 ed.

BEYER, H. L. 2012b. Geospatial Modelling Environment (Version 0.7.3.0). (software). .

BIRDLIFE INTERNATIONAL 2004. Tracking ocean wanderers: the global distribution of albatrosses and petrels. Results from the Global Procellariiform Tracking Workshop.

BIRDLIFE INTERNATIONAL. 2015. *Pterodroma phaeopygia. The IUCN Red List of Threatened Species 2015: e.T22698020A79009412.* [Online]. [Accessed 17/03/2016].

BIRDLIFE INTERNATIONAL. 2016a. *Important Bird and Biodiversity Area factsheet: Round Island* [Online]. BirdLife International. Available: http://www.birdlife.org [Accessed 10/08/2016].

BIRDLIFE INTERNATIONAL. 2016b. *IUCN Red List for birds* [Online]. http://www.birdlife.org Birdlife International. Available: http://www.birdlife.org [Accessed 11/02/16].

BIRDLIFE INTERNATIONAL. 2016c. *Species factsheet: Pterodroma heraldica* [Online]. http://www.birdlife.org. Available: http://www.birdlife.org [Accessed 03/08/2016 2016].

BOGRAD, S. J., BLOCK, B. A., COSTA, D. P. & GODLEY, B. J. 2010. Biologging technologies: new tools for conservation. Introduction. *Endangered Species Research,* 10**,** 1-7.

BOST, C. A., THIEBOT, J. B., PINAUD, D., CHEREL, Y. & TRATHAN, P. N. 2009. Where do penguins go during the inter-breeding period? Using geolocation to track the winter dispersion of the macaroni penguin. *Biology Letters***,** -.

BRETAGNOLLE, V., ATTI, XE & CAROLE 1991. Status of Barau's Petrel (Pterodroma baraui): Colony Sites, Breeding Population and Taxonomic Affinities. *Colonial Waterbirds,* 14**,** 25-33.

BROOKE, M., IMBER, M. & ROWE, G. 2000. Occurrence of two surface-breeding species of Pterodroma on Round Island, Indian Ocean. *Ibis,* 142**,** 154-158.

BROOKE, M. D. 2004. *Albatrosses and Petrels Across the World (Bird Families of the World)*, Oxford University Press, Oxford.

BROOKE, M. D. L. 1995. The breeding biology of the gadfly petrels Pterodroma spp. of the Pitcairn Islands: characteristics, population sizes and controls. *Biological Journal of the Linnean Society,* 56**,** 213-231.

BROOKE, M. D. L. & ROWE, G. 1996. Behavioural and molecular evidence for specific status of light and dark morphs of the Herald Petrel Pterodroma heraldica. *Ibis,* 138**,** 420-432.

BROQUET, T. & PETIT, E. 2004. Quantifying genotyping errors in noninvasive population genetics. *Molecular Ecology,* 13**,** 3601-3608.

BROWN, R. M. 2008. *Molecular ecology of petrels (Pterodroma spp.) from the Indian Ocean and NE Atlantic, and implications for their conservation management.* Doctor of Philosophy, Queen Mary, University of London.

BROWN, R. M., JORDAN, W. C., FAULKES, C. G., JONES, C. G., BUGONI, L., TATAYAH, V., PALMA, R. L. & NICHOLS, R. A. 2011. Phylogenetic Relationships in *Pterodroma* Petrels Are Obscured by Recent Secondary Contact and Hybridization. *PLoS ONE,* 6**,** e20350.

BROWN, R. M., NICHOLS, R. A., FAULKES, C. G., JONES, C. G., BUGONI, L., TATAYAH, V., GOTTELLI, D. & JORDAN, W. C. 2010. Range expansion and hybridization in Round Island petrels (*Pterodroma* spp.): evidence from microsatellite genotypes. *Molecular Ecology,* 19**,** 3157-3170.

BROWN, R. M., TECHOW, N. M., WOOD, A. G. & PHILLIPS, R. A. 2015. Hybridization and Back-Crossing in Giant Petrels (*Macronectes giganteus* and *M. halli*) at Bird Island, South Georgia, and a Summary of Hybridization in Seabirds. *PLoS One,* 10**,** e0121688.

BROWNSTEIN, M. J., CARPTEN, J. D. & SMITH, J. R. 1996. Modulation of non-templated nucleotide addition by Taq DNA polymerase: primer modifications that facilitate genotyping. *BioTechniques,* 20**,** 1004-6, 1008-10.

BURG, T. & CROXALL, J. 2001. Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Molecular Ecology,* 10**,** 2647-2660.

BURKE, C. M. & MONTEVECCHI, W. A. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology,* 278**,** 354-361.

BURNHAM, K. P. & ANDERSON, D. R. 2003. *Model selection and multimodel inference: a practical information-theoretic approach*, Springer Science & Business Media.

BURROWS, M. T., SCHOEMAN, D. S., BUCKLEY, L. B., MOORE, P., POLOCZANSKA, E. S., BRANDER, K. M., BROWN, C., BRUNO, J. F., DUARTE, C. M. & HALPERN, B. S. 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science,* 334**,** 652-655.

CAMPHUYSEN, K., SHAMOUN-BARANES, J., BOUTEN, W. & GARTHE, S. 2012. Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Biological Conservation,* 156**,** 22-29.

CATRY, P., DIAS, M. P., PHILLIPS, R. A. & GRANADEIRO, J. P. 2011. Different Means to the Same End: Long-Distance Migrant Seabirds from Two Colonies Differ in Behaviour, Despite Common Wintering Grounds. *PLoS ONE,* 6**,** e26079.

CATRY, T., RAMOS, J. A., LE CORRE, M. & PHILLIPS, R. A. 2009. Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. *Marine Ecology Progress Series,* 391**,** 231-242.

CECERE, J. G., CALABRESE, L., ROCAMORA, G. & CATONI, C. 2013. Movement Patterns and Habitat Selection of Wedge-tailed Shearwaters (Puffinus pacificus) Breeding at Aride Island, Seychelles. *Waterbirds,* 36**,** 432-437.

CEIA, F. R., PHILLIPS, R. A., RAMOS, J. A., CHEREL, Y., VIEIRA, R. P., RICHARD, P. & XAVIER, J. C. 2012. Short- and long-term consistency in the foraging niche of wandering albatrosses. *Marine Biology,* 159**,** 1581-1591.

CHEKE, A. & HUME, J. P. 2008. *Lost Land of the Dodo: The Ecological history of Mauritius, Reunion and Rodrigues,* United Kingdom, A&C Black.

CHIRGWIN, E., MONRO, K., SGRO, C. M. & MARSHALL, D. J. 2015. Revealing hidden evolutionary capacity to cope with global change. *Global Change Biology,* 21**,** 3356-3366.

CHIUCCHI, J. E. & GIBBS, H. 2010. Similarity of contemporary and historical gene flow among highly fragmented populations of an endangered rattlesnake. *Molecular Ecology,* 19**,** 5345-5358.

CLEELAND, J. B., LEA, M. A. & HINDELL, M. A. 2014. Use of the Southern Ocean by breeding Short-tailed shearwaters (Puffinus tenuirostris). *Journal of Experimental Marine Biology and Ecology,* 450**,** 109-117.

CROXALL, J. & PRINCE, P. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society,* 14**,** 103-131.

CROXALL, J. P., BUTCHART, S. H. M., LASCELLES, B., STATTERSFIELD, A. J., SULLIVAN, B., SYMES, A. & TAYLOR, P. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International,* 22**,** 1-34.

CROXALL, J. P., TRATHAN, P. N. & MURPHY, E. J. 2002. Environmental Change and Antarctic Seabird Populations. *Science,* 297**,** 1510-1514.

CURY, P. M., BOYD, I. L., BONHOMMEAU, S., ANKER-NILSSEN, T., CRAWFORD, R. J. M., FURNESS, R. W., MILLS, J. A., MURPHY, E. J., OSTERBLOM, H., PALECZNY, M., PIATT, J. F., ROUX, J. P., SHANNON, L. & SYDEMAN, W. J. 2011. Global Seabird Response to Forage Fish Depletion-One-Third for the Birds. *Science,* 334**,** 1703-1706.

DAVY, C. M., MARTINEZ-NUNEZ, F., WILLIS, C. K. R. & GOOD, S. V. 2015. Spatial genetic structure among bat hibernacula along the leading edge of a rapidly spreading pathogen. *Conservation Genetics,* 16**,** 1013-1024.

DAWSON, D. A., ÅKESSON, M., BURKE, T., PEMBERTON, J. M., SLATE, J. & HANSSON, B. 2007. Gene Order and Recombination Rate in Homologous Chromosome Regions of the Chicken and a Passerine Bird. *Molecular Biology and Evolution,* 24**,** 1537-1552.

DAWSON, D. A., BREKKE, P., DOS REMEDIOS, N. & HORSBURGH, G. J. 2015. A marker suitable for sex-typing birds from degraded samples. *Conservation Genetics Resources,* 7**,** 337-343.

DAWSON, D. A., HORSBURGH, G. J., KÜPPER, C., STEWART, I. R. K., BALL, A. D., DURRANT, K. L., HANSSON, B., BACON, I. D. A., BIRD, S., KLEIN, Á., KRUPA, A. P., LEE, J.-W., MARTÍ-GÁLVEZ, D., SIMEONI, M., SMITH, G., SPURGIN, L. G. & BURKE, T. 2010. New methods to identify conserved microsatellite loci and develop primer sets of high cross-species utility – as demonstrated for birds. *Molecular Ecology Resources,* 10**,** 475-494.

DEARBORN, D. C., ANDERS, A. D., SCHREIBER, E. A., ADAMS, R. M. M. & MUELLER, U. G. 2003. Inter-island movements and population differentiation in a pelagic seabird. *Molecular Ecology,* 12**,** 2835-2843.

DELMORE, K. E. & IRWIN, D. E. 2014. Hybrid songbirds employ intermediate routes in a migratory divide. *Ecol Lett*.

DEPPE, L., MCGREGOR, K. F., TOMASETTO, F., BRISKIE, J. V. & SCOFIELD, R. P. 2014. Distribution and predictability of foraging areas in breeding Chatham

albatrosses Thalassarche eremita in relation to environmental characteristics. *Marine Ecology Progress Series,* 498**,** 287-301.

DERRAIK, J. G. 2002. The pollution of the marine environment by plastic debris: a review. *Marine pollution bulletin,* 44**,** 842-852.

DEVNEY, C. A., SHORT, M. & CONGDON, B. C. 2009. Sensitivity of tropical seabirds to El Niño precursors. *Ecology,* 90**,** 1175-1183.

DIAS, M. P., GRANADEIRO, J. P. & CATRY, P. 2013. Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. *Animal Behaviour,* 86**,** 359-364.

DURANT, J. M., HJERMANN, D., FREDERIKSEN, M., CHARRASSIN, J. B., LE MAHO, Y., SABARROS, P. S., CRAWFORD, R. J. M. & STENSETH, N. C. 2009. Pros and cons of using seabirds as ecological indicators. *Climate Research,* 39**,** 115-129.

DURANT, J. M., HJERMANN, D. Ø., OTTERSEN, G. & STENSETH, N. C. 2007. Climate and the match or mismatch between predator requirements and resource availability.

EARL, D. A. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation genetics resources,* 4**,** 359-361.

EKSTROM, P. A. 2004. An advance in geolocation by light. *Memoirs of the National Insitute of Polar Research,* Special Issue 210–226.

ELLEGREN, H., PRIMMER, C. & SHELDON, B. 1995. Microsatellite 'evolution': directionality or bias? *Nature Genetics,* 11**,** 360-362.

EVANNO, G., REGNAUT, S. & GOUDET, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol Ecol,* 14**,** 2611-20.

FALUSH, D., STEPHENS, M. & PRITCHARD, J. 2003. Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics,* 164.

FAUBET, P., WAPLES, R. S. & GAGGIOTTI, O. E. 2007. Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. *Molecular Ecology,* 16**,** 1149-1166.

FAYET, A. L., FREEMAN, R., SHOJI, A., PADGET, O., PERRINS, C. M. & GUILFORD, T. 2015. Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird. *Animal Behaviour,* 110**,** 79-89.

FINKELSTEIN, M., KEITT, B. S., CROLL, D. A., TERSHY, B., JARMAN, W. M., RODRIGUEZ-PASTOR, S., ANDERSON, D. J., SIEVERT, P. R. & SMITH, D. R. 2006. Albatross Species Demonstrate Regional Differences In North Pacific Marine Contamination. *Ecological Applications,* 16**,** 678-686.

FORERO, M. G., BORTOLOTTI, G. R., HOBSON, K. A., DONAZAR, J. A., BERTELLOTI, M. & BLANCO, G. 2004. High Trophic Overlap within the Seabird Community of Argentinean Patagonia: A Multiscale Approach. *Journal of Animal Ecology,* 73**,** 789-801.

FOX, J. W. & PHILLIPS, R. A. 2010. Geolocator manual v8 (March 2010). *http://www.antarctica.ac.uk/engineering/geo_downloads/Geolocator_manual_v8.pdf, download on,* 25**,** 2011.

FREDERIKSEN, M., HARRIS, M. P., DAUNT, F., ROTHERY, P. & WANLESS, S. 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. *Global Change Biology,* 10**,** 1214-1221.

FREDERIKSEN, M., MOE, B., DAUNT, F., PHILLIPS, R. A., BARRETT, R. T., BOGDANOVA, M. I., BOULINIER, T., CHARDINE, J. W., CHASTEL, O., CHIVERS, L. S., CHRISTENSEN-DALSGAARD, S., CLÉMENT-CHASTEL, C., COLHOUN, K., FREEMAN, R., GASTON, A. J., GONZÁLEZ-SOLÍS, J., GOUTTE, A., GRÉMILLET, D., GUILFORD, T., JENSEN, G. H., KRASNOV, Y., LORENTSEN, S.-H., MALLORY, M. L., NEWELL, M., OLSEN, B., SHAW, D., STEEN, H., STRØM, H., SYSTAD, G. H., THÓRARINSSON, T. L. & ANKER-NILSSEN, T. 2012. Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions,* 18**,** 530-542.

FREEMAN, R., DENNIS, T., LANDERS, T., THOMPSON, D., BELL, E., WALKER, M. & GUILFORD, T. 2010. Black Petrels (Procellaria parkinsoni) Patrol the Ocean Shelf-Break: GPS Tracking of a Vulnerable Procellariiform Seabird. *Plos One,* 5.

FRIESEN, V. 2015. Speciation in seabirds: why are there so many species…and why aren't there more? *Journal of Ornithology***,** 1-13.

FRIESEN, V. L., BURG, T. M. & MCCOY, K. D. 2007a. Mechanisms of population differentiation in seabirds. *Mol Ecol,* 16**,** 1765-85.

FRIESEN, V. L., SMITH, A. L., GOMEZ-DIAZ, E., BOLTON, M., FURNESS, R. W., GONZALEZ-SOLES, J. & MONTEIRO, L. R. 2007b. Sympatric speciation by allochrony in a seabird. *Proceedings of the National Academy of Sciences,* 104**,** 18589-18594.

FUDICKAR, A. M., WIKELSKI, M. & PARTECKE, J. 2012. Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution,* 3**,** 47-52.

GAME, E. T., GRANTHAM, H. S., HOBDAY, A. J., PRESSEY, R. L., LOMBARD, A. T., BECKLEY, L. E., GJERDE, K., BUSTAMANTE, R., POSSINGHAM, H. P. & RICHARDSON, A. J. 2009. Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution,* 24**,** 360-369.

GARANT, D., FORDE, S. E. & HENDRY, A. P. 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology,* 21**,** 434-443.

GARNETT, S. & CROWLEY, G. 2000. The Action Plan for Australian Birds 2000.[Online]. Canberra: Environment Australia and Birds Australia.

GARNETT, S., SZABO, J. & DUTSON, G. 2011. Action Plan for Australian Birds 2010.

GENOVART, M., THIBAULT, J.-C., IGUAL, J. M., BAUZÀ-RIBOT, M. D. M., RABOUAM, C. & BRETAGNOLLE, V. 2013. Population Structure and Dispersal Patterns within and between Atlantic and Mediterranean Populations of a Large-Range Pelagic Seabird. *Plos One,* 8**,** e70711.

GIBBS, M., DAWSON, D. A., MCCAMLEY, C., WARDLE, A. F., BURKE, T. & ARMOUR, J. A. L. 1997. Chicken microsatellite markers isolated from libraries enriched for simple tandem repeats. *Animal Genetics,* 28**,** 401-417.

GLENN, T. C. & SCHABLE, N. A. 2005. Isolating Microsatellite DNA Loci. *Methods in Enzymology.* Academic Press.

GÓMEZ-DÍAZ, E., GONZÁLEZ-SOLÍS, J. & PEINADO, M. 2009. Population structure in a highly pelagic seabird, the Cory's shearwater *Calonectris diomedea*: an examination of genetics, morphology and ecology. *Marine Ecology Progress Series,* 382**,** 197-209.

GOOD, T., ELLIS, J., ANNETT, C. & PIEROTTI, R. 2000. BOUNDED HYBRID SUPERIORITY IN AN AVIAN HYBRID ZONE: EFFECTS OF MATE, DIET, AND HABITAT CHOICE. *Evolution,* 54**,** 1774-1783.

GOUDET, J., PERRIN, N. & WASER, P. 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology,* 11**,** 1103-1114.

GRANT, P. R. & GRANT, R. 1992. Hybridization of bird species. *Science,* 256**,** 193.

GRECIAN, W. J., WITT, M. J., ATTRILL, M. J., BEARHOP, S., GODLEY, B. J., GRÉMILLET, D., HAMER, K. C. & VOTIER, S. C. 2012. A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern gannets breeding in the North East Atlantic. *Biological Conservation,* 156**,** 43-52.

GRÉMILLET, D. & BOULINIER, T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology Progress Series,* 391**,** 121-137.

GUILFORD, T., FREEMAN, R., BOYLE, D., DEAN, B., KIRK, H., PHILLIPS, R. & PERRINS, C. 2011. A Dispersive Migration in the Atlantic Puffin and Its Implications for Migratory Navigation. *PLoS ONE,* 6**,** e21336.

GUILFORD, T., WYNN, R., MCMINN, M., RODRÃGUEZ, A., FAYET, A., MAURICE, L., JONES, A. & MEIER, R. 2012. Geolocators Reveal Migration and Pre-Breeding Behaviour of the Critically Endangered Balearic Shearwater <italic>Puffinus mauretanicus</italic>. *PLoS ONE,* 7**,** e33753.

GUTOWSKY, S. E., LEONARD, M., CONNERS, M., SHAFFER, S. & JONSEN, I. 2015. Individual-level variation and higher-level interpretations of space use in wide-ranging species: An albatross case study of sampling effects. *Frontiers in Marine Science,* 2.

GUTOWSKY, S. E., TREMBLAY, Y., KAPPES, M. A., FLINT, E. N., KLAVITTER, J., LANIAWE, L., COSTA, D. P., NAUGHTON, M. B., ROMANO, M. D. & SHAFFER, S. A. 2014. Divergent post-breeding distribution and habitat associations of fledgling and adult Black-footed Albatrosses Phoebastria nigripes in the North Pacific. *Ibis,* 156**,** 60-72.

HALPERN, B. S., WALBRIDGE, S., SELKOE, K. A., KAPPEL, C. V., MICHELI, F., D'AGROSA, C., BRUNO, J. F., CASEY, K. S., EBERT, C., FOX, H. E., FUJITA, R., HEINEMANN, D., LENIHAN, H. S., MADIN, E. M., PERRY, M. T., SELIG, E. R., SPALDING, M., STENECK, R. & WATSON, R. 2008. A global map of human impact on marine ecosystems. *Science,* 319**,** 948-52.

HARRISON, J. M. & HARRISON, J. G. 1965. A presumed trigen duck involving mallard, pintail and gadwall. *Bulletin of The British Ornithologists' Club,* 85**,** 22-26.

HEDD, A., GALES, R. & BROTHERS, N. 2001. Foraging strategies of shy albatross Thalassarche cauta breeding at Albatross Island, Tasmania, Australia. *Marine Ecology Progress Series,* 224**,** 267-282.

HENNICKE, J. C. & WEIMERSKIRCH, H. 2014. Coping with variable and oligotrophic tropical waters: foraging behaviour and flexibility of the Abbott's booby Papasula abbotti. *Marine Ecology Progress Series,* 499**,** 259-273.

HICKLING, R., ROY, D., HILL, J., FOX, R. & THOMAS, C. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global change biology,* 12**,** 450-455.

HILL, R. D. 1994. Theory of geolocation by light levels. *In:* LE BOEUF, B. J. & LAWS, R. M. (eds.) *Elephant seals: population ecology, behavior, and physiology.* Berkeley: University of California Press.

HILL, R. D. & BRAUN, M. J. 2001. Geolocation by light level. *Electronic tagging and tracking in marine fisheries.* Springer.

HOEGH-GULDBERG, O. & BRUNO, J. F. 2010. The impact of climate change on the world's marine ecosystems. *Science,* 328**,** 1523-1528.

HOLDAWAY, R. N., WORTHY, T. H. & TENNYSON, A. J. 2001. A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand journal of zoology,* 28**,** 119-187.

HUBBS, C. L. 1955. Hybridization between fish species in nature. *Systematic zoology,* 4**,** 1-20.

HUIN, N. 2002. Foraging distribution of the black-browed albatross,Thalassarche melanophris, breeding in the Falkland Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 12**,** 89-99.

HYRENBACH, K. D., FERNÁNDEZ, P. & ANDERSON, D. J. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series,* 233**,** 283-301.

IMBER, M. 2004. Kermadec petrels (*Pterodroma neglecta*) at Ilha da Trindade, South Atlantic Ocean and in the North Atlantic. *Notornis,* 51**,** 33-40.

IMBER, M. 2005. A response to M. Tove's rebuttal of Imber (2004). *Notornis,* 52**,** 58-59.

IMBER, M. J. 2008. Kermadec Petrels (*Pterodroma neglecta*) off the Azores, North Atlantic ocean. *Notornis,* 55**,** 106-108.

ISAAC, N. J. B., MALLET, J. & MACE, G. M. 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology & Evolution,* 19**,** 464-469.

JAKOBSSON, M. & ROSENBERG, N. A. 2007. CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics,* 23.

JAQUEMET, S., LE CORRE, M. & QUARTLY, G. D. 2007. Ocean control of the breeding regime of the sooty tern in the southwest Indian Ocean. *Deep Sea Research Part I: Oceanographic Research Papers,* 54**,** 130-142.

JOHNSON, P. C. & HAYDON, D. T. 2007. Maximum-likelihood estimation of allelic dropout and false allele error rates from microsatellite genotypes in the absence of reference data. *Genetics,* 175**,** 827-842.

JURY, M. R. & PATHACK, B. 1991. A study of climate and weather variability over the tropical southwest Indian Ocean. *Meteorology and Atmospheric Physics,* 47**,** 37-48.

KAEUFFER, R., REALE, D., COLTMAN, D. W. & PONTIER, D. 2007. Detecting population structure using STRUCTURE software: effect of background linkage disequilibrium. *Heredity,* 99**,** 374-380.

KALINOWSKI, S. T., TAPER, M. L. & MARSHALL, T. C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol,* 16**,** 1099-106.

KAPPES, M. A., WEIMERSKIRCH, H., PINAUD, D. & LE CORRE, M. 2011. Variability of resource partitioning in sympatric tropical boobies. *Marine Ecology Progress Series,* 441**,** 281-294.

KENTA, T., GRATTEN, J., HAIGH, N. S., HINTEN, G. N., SLATE, J., BUTLIN, R. K. & BURKE, T. 2008. Multiplex SNP-SCALE: a cost-effective medium-throughput single nucleotide polymorphism genotyping method. *Molecular Ecology Resources,* 8**,** 1230-1238.

KING, B. & REIMER, D. 1991. Breeding and Behavior of the Herald Petrel *Pterodroma arminjoniana* on Raine Island, Queensland. *Emu,* 91**,** 122-125.

KÜPPER, C., HORSBURGH, G. J., DAWSON, D. A., FFRENCH-CONSTANT, R., SZÉKELY, T. & BURKE, T. 2007. Characterization of 36 polymorphic microsatellite loci in the Kentish plover (*Charadrius alexandrinus*) including two sex-linked loci and their amplification in four other Charadrius species. *Molecular Ecology Notes,* 7**,** 35-39.

LAM, C. H., NIELSEN, A. & SIBERT, J. R. 2010. Incorporating sea-surface temperature to the light-based geolocation model TrackIt. *Marine Ecology Progress Series,* 419**,** 71-84.

LASCELLES, B. G., LANGHAM, G. M., RONCONI, R. A. & REID, J. B. 2012. From hotspots to site protection: Identifying Marine Protected Areas for seabirds around the globe. *Biological Conservation,* 156**,** 5-14.

LASCELLES, B. G., TAYLOR, P. R., MILLER, M. G. R., DIAS, M. P., OPPEL, S., TORRES, L., HEDD, A., LE CORRE, M., PHILLIPS, R. A., SHAFFER, S. A., WEIMERSKIRCH, H., SMALL, C. & VISCONTI, P. 2016. Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions,* 22**,** 422-431.

LE CORRE, M. 2001. Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. *Journal of Zoology,* 254**,** 239-249.

LE CORRE, M., JAEGER, A., PINET, P., KAPPES, M. A., WEIMERSKIRCH, H., CATRY, T., RAMOS, J. A., RUSSELL, J. C., SHAH, N. & JAQUEMET, S. 2012. Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. *Biological Conservation,* 156**,** 83-93.

LÉVY, M., SHANKAR, D., ANDRÉ, J., SHENOI, S., DURAND, F. & DE BOYER MONTÉGUT, C. 2007. Basin-wide seasonal evolution of the Indian Ocean's phytoplankton blooms. *Journal of Geophysical Research,* 112.

LEWIS, S., SHERRATT, T. N., HAMER, K. C. & WANLESS, S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature,* 412**,** 816-819.

LISOVSKI, S. & HAHN, S. 2012. GeoLight–processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution,* 3**,** 1055-1059.

LISOVSKI, S., HEWSON, C. M., KLAASSEN, R. H. G., KORNER-NIEVERGELT, F., KRISTENSEN, M. W. & HAHN, S. 2012. Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution,* 3**,** 603-612.

MACE, G. M. 2004. The role of taxonomy in species conservation. *Philos Trans R Soc Lond B Biol Sci,* 359**,** 711-9.

MADEIROS, J., CARLILE, N. & PRIDDEL, D. 2012. Breeding biology and population increase of the Endangered Bermuda Petrel Pterodroma cahow. *Bird Conservation International,* 22**,** 35-45.

MALLET, J. 2005. Hybridization as an invasion of the genome. *Trends in Ecology & Evolution,* 20**,** 229-237.

MARIE, A. D., BERNATCHEZ, L. & GARANT, D. 2011. Empirical assessment of software efficiency and accuracy to detect introgression under variable stocking scenarios in brook charr (*Salvelinus fontinalis*). *Conservation Genetics,* 12**,** 1215-1227.

MAXWELL, S. M. & MORGAN, L. E. 2013. Foraging of seabirds on pelagic fishes: implications for management of pelagic marine protected areas. *Marine Ecology Progress Series,* 481**,** 289-303.

MCCARTHY, E. M. 2006. *Handbook of avian hybrids of the world*, Oxford University Press.

MCCRACKEN, K. G. & WILSON, R. E. 2011. Gene Flow and Hybridization between Numerically Imbalanced Populations of Two Duck Species in the Falkland Islands. *PLoS ONE,* 6**,** e23173.

MEIRMANS, P. G. 2014. Nonconvergence in Bayesian estimation of migration rates. *Molecular Ecology Resources,* 14**,** 726-733.

MENDEZ, L., COTTÉ, C., PRUDOR, A. & WEIMERSKIRCH, H. 2016. Variability in foraging behaviour of red-footed boobies nesting on Europa Island. *Acta Oecologica,* 72**,** 87-97.

MERTON, D. 1987. Eradication of rabbits from Round Island, Mauritius: a conservation success story. *Dodo,* 24**,** 19-43.

MILOT, E., WEIMERSKIRCH, H. & BERNATCHEZ, L. 2008. The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but philopatric albatross species. *Mol Ecol,* 17**,** 1658-73.

MONTICELLI, D., RAMOS, J. & QUARTLY, G. 2007. Effects of annual changes in primary productivity and ocean indices on the breeding performance of tropical roseate terns in the western Indian Ocean. *Marine Ecology Progress Series*.

MOORE, P. J., TAYLOR, G. A. & AMEY, J. M. 1997. Interbreeding of black-browed albatross *Diomedea m. melanophris* and New Zealand black-browed albatross *D. m. impavida* on Campbell Island. *EMU-NORTH MELBOURNE-,* 97**,** 322-323.

MORRIS-POCOCK, J. A., STEEVES, T. E., ESTELA, F. A., ANDERSON, D. J. & FRIESEN, V. L. 2010. Comparative phylogeography of brown (*Sula leucogaster*) and red-footed boobies (*S. sula*): The influence of physical barriers and habitat preference on gene flow in pelagic seabirds. *Molecular Phylogenetics and Evolution,* 54**,** 883-896.

MURPHY, R. C. & PENNOYER, J. M. 1952. Larger petrels of the genus Pterodroma. American Museum novitates; no. 1580.

NAVARRO, J., CARDADOR, L., BROWN, R. & PHILLIPS, R. A. 2015. Spatial distribution and ecological niches of non-breeding planktivorous petrels. *Scientific Reports,* 5**,** 12164.

NAVARRO, J., FORERO, M. G., GONZÁLEZ-SOLÍS, J., IGUAL, J. M., BÉCARES, J. & HOBSON, K. A. 2009d. Foraging segregation between two closely related shearwaters breeding in sympatry. *Biology Letters,* 5**,** 545-548.

NAVARRO, J. & GONZLEZ-SOLIS, J. 2009b. Environmental determinants of foraging strategies in Cory's shearwaters Calonectris diomedea. *Marine Ecology Progress Series,* 378**,** 259-267.

NAVARRO, J., MORENO, R., BRAUN, L., SANPERA, C. & HENNICKE, J. C. 2014. Resource partitioning between incubating and chick-rearing brown boobies and red-tailed tropicbirds on Christmas Island. *Zoological Studies,* 53**,** 1-6.

NAVARRO, J., VOTIER, S. C., AGUZZI, J., CHIESA, J. J., FORERO, M. G. & PHILLIPS, R. A. 2013. Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. *Plos One,* 8**,** e62897.

NICHOLLS, J. A., DOUBLE, M. C., ROWELL, D. M. & MAGRATH, R. D. 2000. The evolution of cooperative and pair breeding in thornbills Acanthiza (Pardalotidae). *Journal of Avian Biology,* 31**,** 165-176.

NICOLL, M. A. C., NEVOUX, M., JONES, C. G., RATCLIFFE, N., RUHOMAUN, K., TATAYAH, V. & NORRIS, K. 2016. Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology***,** n/a-n/a.

NIELSEN, A., BIGELOW, K. A., MUSYL, M. K. & SIBERT, J. R. 2006. Improving light-based geolocation by including sea surface temperature. *Fisheries Oceanography,* 15**,** 314-325.

NOSIL, P. 2008. Speciation with gene flow could be common. *Molecular Ecology,* 17**,** 2103-2106.

O'BRIEN, S. H., WEBB, A., BREWER, M. J. & REID, J. B. 2012. Use of kernel density estimation and maximum curvature to set Marine Protected Area boundaries: Identifying a Special Protection Area for wintering red-throated divers in the UK. *Biological Conservation,* 156**,** 15-21.

OLAH, G., BUTCHART, S. H. M., SYMES, A., GUZMÁN, I. M., CUNNINGHAM, R., BRIGHTSMITH, D. J. & HEINSOHN, R. 2016. Ecological and socio-economic factors affecting extinction risk in parrots. *Biodiversity and Conservation,* 25**,** 205-223.

OPPEL, S., BEARD, A., FOX, D., MACKLEY, E., LEAT, E., HENRY, L., CLINGHAM, E., FOWLER, N., SIM, J., SOMMERFELD, J., WEBER, N., WEBER, S. & BOLTON, M. 2015. Foraging distribution of a tropical seabird supports Ashmole's hypothesis of population regulation. *Behavioral Ecology and Sociobiology***,** 1-12.

ORIANS, G. H. & PEARSON, N. E. 1979. On the theory of central place foraging. *Analysis of ecological systems. Ohio State University Press, Columbus***,** 155-177.

PAIVA, V. H., GERALDES, P., RAMÍREZ, I., MEIRINHO, A., GARTHE, S. & RAMOS, J. A. 2010a. Foraging plasticity in a pelagic seabird species along a marine productivity gradient. *Marine Ecology Progress Series,* 398**,** 259-274.

PAIVA, V. H., GERALDES, P., RAMÍREZ, I., MEIRINHO, A., GARTHE, S. & RAMOS, J. A. 2010b. Oceanographic characteristics of areas used by Cory's shearwaters during short and long foraging trips in the North Atlantic. *Marine Biology,* 157**,** 1385-1399.

PAIVA, V. H., GERALDES, P., RAMIREZ, I., WERNER, A. C., GARTHE, S. & RAMOS, J. A. 2013. Overcoming difficult times: the behavioural resilience of a marine predator when facing environmental stochasticity. *Marine Ecology Progress Series,* 486**,** 277-288.

PALECZNY, M., HAMMILL, E., KARPOUZI, V. & PAULY, D. 2015. Population Trend of the World's Monitored Seabirds, 1950-2010. *PLoS ONE,* 10**,** e0129342.

PARSON, L. M. & EVANS, A. J. 2005. Seafloor topography and tectonic elements of the Western Indian Ocean. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences,* 363**,** 15-24.

PATRICK, S. C., BEARHOP, S., GRÉMILLET, D., LESCROËL, A., GRECIAN, W. J., BODEY, T. W., HAMER, K. C., WAKEFIELD, E., LE NUZ, M. & VOTIER, S. C. 2013. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos,* 123**,** 33-40.

PATRICK, S. C. & WEIMERSKIRCH, H. 2014. Personality, Foraging and Fitness Consequences in a Long Lived Seabird. *Plos One,* 9**,** e87269.

PÉRON, C. 2013. Tracking through Life Stages: Adult, Immature and Juvenile Autumn Migration in a Long-Lived Seabird. *Plos One,* 8**,** e72713.

PHILLIPS, R. A., MCGILL, R. A. R., DAWSON, D. A. & BEARHOP, S. 2011. Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Marine Biology,* 158**,** 2199-2208.

PHILLIPS, R. A., SILK, J. R. D., CROXALL, J. P., AFANASYEV, V. & BRIGGS, D. R. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series,* 266**,** 265-272.

PIATT, I. J. F., SYDEMAN, W. J. & WIESE, F. 2007. Introduction: seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series,* 352**,** 199-204.

PINAUD, D., CHEREL, Y. & WEIMERSKIRCH, H. 2005a. Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Marine Ecology Progress Series,* 298**,** 295-304.

PINAUD, D. & WEIMERSKIRCH, H. 2005b. Scale-Dependent Habitat Use in a Long-Ranging Central Place Predator. *Journal of Animal Ecology,* 74**,** 852-863.

PINAUD, D. & WEIMERSKIRCH, H. 2007. At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *Journal of Animal Ecology,* 76**,** 9-19.

PINET, P., JAEGER, A., CORDIER, E., POTIN, G. L. & LE CORRE, M. 2011b. Celestial Moderation of Tropical Seabird Behavior. *PLoS ONE,* 6**,** e27663.

PINET, P., JAQUEMET, S., PHILLIPS, R. A. & CORRE, M. 2012a. Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Anim Behav,* 83.

PINET, P., JAQUEMET, S., PINAUD, D., WEIMERSKIRCH, H., RICHARD A. PHILLIPS, R. & LE CORRE, M. 2011a. Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel Pterodroma baraui. *Marine Ecology Progress Series,* 423.

PINET, P., JAQUEMET, S. B., PHILLIPS, R. A. & LE CORRE, M. 2012b. Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Animal Behaviour*.

POTIER, S., CARPENTIER, A., GRÉMILLET, D., LEROY, B. & LESCROËL, A. 2015. Individual repeatability of foraging behaviour in a marine predator, the great cormorant, Phalacrocorax carbo. *Animal Behaviour,* 103**,** 83-90.

PRITCHARD, J., STEPHENS, M. & DONNELLY, P. 2000. Inference of population structure using multilocus genotype data. *Genetics,* 155**,** 945 - 959.

QUILLFELDT, P., PHILLIPS, R. A., MARX, M. & MASELLO, J. F. 2014. Colony attendance and at-sea distribution of thin-billed prions during the early breeding season. *Journal of Avian Biology*, no-no.

R DEVELOPMENT CORE TEAM. 2013. *R: A language and environment for statistical computing* [Online]. Vienna, Austria: R Foundation for Statistical Computing. Available: http://www.R-project.org/ [Accessed 09/05/2013].

RAKHIMBERDIEV, E., WINKLER, D., BRIDGE, E., SEAVY, N., SHELDON, D., PIERSMA, T. & SAVELIEV, A. 2015. A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. *Movement Ecology,* 3**,** 1-15.

RAMÍREZ, I., PAIVA, V. H., FAGUNDES, I., MENEZES, D., SILVA, I., CEIA, F. R., PHILLIPS, R. A., RAMOS, J. A. & GARTHE, S. 2015. Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Animal Conservation*, n/a-n/a.

RAMÍREZ, I., PAIVA, V. H., MENEZES, D., SILVA, I., PHILLIPS, R. A., RAMOS, J. A. & GARTHE, S. 2013. Year-round distribution and habitat preferences of the Bugio petrel. *Marine Ecology Progress Series,* 476**,** 269-284.

RAMOS, R., RAMÍREZ, I., PAIVA, V. H., MILITÃO, T., BISCOITO, M., MENEZES, D., PHILLIPS, R. A., ZINO, F. & GONZÁLEZ-SOLÍS, J. 2016. Global spatial ecology of three closely-related gadfly petrels. *Scientific Reports,* 6**,** 23447.

RANDLER, C. 2002. Avian hybridization, mixed pairing and female choice. *Animal Behaviour,* 63**,** 103-119.

RANDLER, C. 2006. Behavioural and ecological correlates of natural hybridization in birds. *Ibis,* 148**,** 459-467.

RANNALA, B. 2012. BayesAss edition 3.0 user's manual. *Accessed online,* 27.

RAYMOND, M. & ROUSSET, F. 1995. GENEPOP (Version 1.2): Population Genetics Software for Exact Tests and Ecumenicism. *Journal of Heredity,* 86**,** 248-249.

RAYNER, M. J., HAUBER, M. E., CLOUT, M. N., SELDON, D. S., VAN DIJKEN, S., BURY, S. & PHILLIPS, R. A. 2008. Foraging ecology of the Cook's petrel Pterodroma cookii during the austral breeding season: a comparison of its two populations. *Marine Ecology Progress Series,* 370**,** 271-284.

RAYNER, M. J., HAUBER, M. E., STEEVES, T. E., LAWRENCE, H. A., THOMPSON, D. R., SAGAR, P. M., BURY, S. J., LANDERS, T. J., PHILLIPS, R. A., RANJARD, L. & SHAFFER, S. A. 2011. Contemporary and historical separation of transequatorial migration between genetically distinct seabird populations. *Nat Commun,* 2**,** 332.

RAYNER, M. J., TAYLOR, G. A., GUMMER, H. D., PHILLIPS, R. A., SAGAR, P. M., SHAFFER, S. A. & THOMPSON, D. R. 2012. The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (Pterodroma axillaris). *Emu*, -.

REED, D. H. & FRANKHAM, R. 2003. Correlation between fitness and genetic diversity. *Conservation biology,* 17**,** 230-237.

REED, T. E., WAPLES, R. S., SCHINDLER, D. E., HARD, J. J. & KINNISON, M. T. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. *Proc Biol Sci,* 277**,** 3391-400.

REID, T. A., TUCK, G. N., HINDELL, M. A., THALMANN, S., PHILLIPS, R. A. & WILCOX, C. 2013. Nonbreeding distribution of flesh-footed shearwaters and the

potential for overlap with north Pacific fisheries. *Biological Conservation,* 166**,** 3-10.

RENFREW, R. B., KIM, D., PERLUT, N., SMITH, J., FOX, J. & MARRA, P. P. 2013. Phenological matching across hemispheres in a long-distance migratory bird. *Diversity and Distributions***,** n/a-n/a.

RHYMER, J. M. & SIMBERLOFF, D. 1996. Extinction by Hybridization and Introgression. *Annual Review of Ecology and Systematics,* 27**,** 83-109.

ROBERTSON, G. S., BOLTON, M., GRECIAN, W. J., WILSON, L. J., DAVIES, W. & MONAGHAN, P. 2014. Resource partitioning in three congeneric sympatrically breeding seabirds: Foraging areas and prey utilization. *The Auk,* 131**,** 434-446.

RONCONI, R. A., LASCELLES, B. G., LANGHAM, G. M., REID, J. B. & ORO, D. 2012. The role of seabirds in Marine Protected Area identification, delineation, and monitoring: Introduction and synthesis. *Biological Conservation,* 156**,** 1-4.

ROSENBERG, N. A. 2004. DISTRUCT: a program for the graphical display of population structure. *Molecular Ecology Notes,* 4**,** 137-138.

ROYLE, N. J., HILL, M. C. & JEFFREYS, A. J. 1992. Isolation of Telomere Junction Fragments by Anchored Polymerase Chain Reaction. *Proceedings of the Royal Society of London B: Biological Sciences,* 247**,** 57-67.

ROZEN, S. & SKALETSKY, H. 2000. *In: Bioinformatics methods and protocols: Methods in molecular biology,* Totowa, NJ, Humana Press.

SCHAEFER, K. M., FULLER, D. W. & BLOCK, B. A. 2011. Movements, behavior, and habitat utilization of yellowfin tuna (Thunnus albacares) in the Pacific Ocean off Baja California, Mexico, determined from archival tag data analyses, including unscented Kalman filtering. *Fisheries Research,* 112**,** 22-37.

SCHLUTER, D. 2009. Evidence for Ecological Speciation and Its Alternative. *Science,* 323**,** 737-741.

SCHOTT, F. A. & MCCREARY JR, J. P. 2001. The monsoon circulation of the Indian Ocean. *Progress in Oceanography,* 51**,** 1-123.

SEAVY, N. E., HUMPLE, D. L., CORMIER, R. L. & GARDALI, T. 2012. Establishing the Breeding Provenance of a Temperate-Wintering North American Passerine, the Golden-Crowned Sparrow, Using Light-Level Geolocation. *Plos One,* 7**,** e34886.

SEUTIN, G., WHITE, B. N. & BOAG, P. T. 1991. Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology,* 69**,** 82-90.

SILVA, M. F., SMITH, A. L., FRIESEN, V. L., BRIED, J., HASEGAWA, O., COELHO, M. M. & SILVA, M. C. 2016. Mechanisms of global diversification in the marine species Madeiran Storm-petrel Oceanodroma castro and Monteiro's Storm-petrel O. monteiroi: Insights from a multi-locus approach. *Molecular Phylogenetics and Evolution,* 98**,** 314-323.

SLATE, J., HALE, M. C. & BIRKHEAD, T. R. 2007. Simple sequence repeats in zebra finch (Taeniopygia guttata) expressed sequence tags: a new resource for evolutionary genetic studies of passerines. *BMC Genomics,* 8**,** 1-12.

SMADJA, C. M. & BUTLIN, R. K. 2011. A framework for comparing processes of speciation in the presence of gene flow. *Molecular Ecology,* 20**,** 5123-5140.

SOANES, L. M., BRIGHT, J. A., CARTER, D., DIAS, M. P., FLEMING, T., GUMBS, K., HUGHES, G., MUKHIDA, F. & GREEN, J. A. 2016. Important foraging areas of

seabirds from Anguilla, Caribbean: Implications for marine spatial planning. *Marine Policy,* 70**,** 85-92.

SOMMERFELD, J. & HENNICKE, J. C. 2010. Comparison of trip duration, activity pattern and diving behaviour by Red-tailed Tropicbirds (Phaethon rubricauda) during incubation and chick-rearing. *Emu,* 110**,** 78-86.

SOMMERFELD, J., KATO, A., ROPERT-COUDERT, Y., GARTHE, S., WILCOX, C. & HINDELL, M. A. 2015. Flexible foraging behaviour in a marine predator, the Masked booby (Sula dactylatra), according to foraging locations and environmental conditions. *Journal of Experimental Marine Biology and Ecology,* 463**,** 79-86.

SPEAR, L. B. & AINLEY, D. G. 1997. Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis,* 139**,** 221-233.

SPEAR, L. B., AINLEY, D. G. & RIBIC, C. A. 1995. Incidence of plastic in seabirds from the tropical pacific, 1984–1991: relation with distribution of species, sex, age, season, year and body weight. *Marine Environmental Research,* 40**,** 123-146.

STAUB, C. G., STEVENS, F. R. & WAYLEN, P. R. 2014. The geography of rainfall in Mauritius: Modelling the relationship between annual and monthly rainfall and landscape characteristics on a small volcanic island. *Applied Geography,* 54**,** 222-234.

STEEVES, T. E., ANDERSON, D. J. & FRIESEN, V. L. 2005. A role for nonphysical barriers to gene flow in the diversification of a highly vagile seabird, the masked booby (*Sula dactylatra*). *Mol Ecol,* 14**,** 3877-87.

SUMNER, M. & WOTHERSPOON, S. 2012. tripEstimation: Metropolis sampler and supporting functions for estimating animal movement from archival tags and satellite fixes. R package version 0.0-38 ed.

SUMNER, M., WOTHERSPOON, S. & HINDELL, M. 2009. Bayesian Estimation of Animal Movement from Archival and Satellite Tags. *PLoS ONE,* 4**,** e7234-e.

SURMAN, C. A., NICHOLSON, L. W. & SANTORA, J. A. 2012. Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. *Marine Ecology-Progress Series,* 454**,** 147-157.

SURYAN, R. M., DIETRICH, K. S., MELVIN, E. F., BALOGH, G. R., SATO, F. & OZAKI, K. 2007. Migratory routes of short-tailed albatrosses: Use of exclusive economic zones of North Pacific Rim countries and spatial overlap with commercial fisheries in Alaska. *Biological Conservation,* 137**,** 450-460.

SURYAN, R. M., SATO, F., BALOGH, G. R., HYRENBACH, K. D., SIEVERT, P. R. & OZAKI, K. 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. *Deep Sea Research Part II: Topical Studies in Oceanography,* 53**,** 370-386.

TABERLET, P., GRIFFIN, S., GOOSSENS, B., QUESTIAU, S., MANCEAU, V., ESCARAVAGE, N., WAITS, L. P. & BOUVET, J. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic acids research,* 24**,** 3189-3194.

TATAYAH, R. V. V. 2010. *The breeding biology of the Round Island Petrel.* University of Mauritius.

TAYLOR, G., COCKBURN, S., PALMER, D. & LIDDY, P. 2012. Breeding activity of Chatham Island taiko (Pterodroma magentae) monitored using PIT tag recorders. *New Zealand Journal of Ecology,* 36**,** 425–432.

TENNYSON, A. J. D., LAWRENCE, H. A., TAYLOR, G. A. & IMBER, M. J. 2013. A hybrid gadfly petrel suggests that soft-plumaged petrels (*Pterodroma mollis*) had colonised the Antipodes Islands by the 1920s. *Notornis,* 60**,** 290-295.

THAXTER, C. B., LASCELLES, B., SUGAR, K., COOK, A. S. C. P., ROOS, S., BOLTON, M., LANGSTON, R. H. W. & BURTON, N. H. K. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation,* 156**,** 53-61.

THIEBOT, J. B. & PINAUD, D. 2010. Quantitative method to estimate species habitat use from light-based geolocation data. *Endangered Species Research,* 10**,** 341-353.

THIERS, L., DELORD, K., BARBRAUD, C., PHILLIPS, R. A., PINAUD, D. & WEIMERSKIRCH, H. 2014. Foraging zones of the two sibling species of giant petrels in the Indian Ocean throughout the annual cycle: implication for their conservation. *Marine Ecology Progress Series,* 499**,** 233-248.

TOMPKINS, D., MITCHELL, R. & BRYANT, D. 2006. Hybridization increases measures of innate and cell-mediated immunity in an endangered bird species. *Journal of animal ecology,* 75**,** 559-564.

TOVE, M. H. 2005. Kermadec Petrels (*Pterodroma neglecta*) in the Atlantic Ocean–a rebuttal. *Notornis,* 52**,** 56-58.

VÄHÄ, J. P. & PRIMMER, C. R. 2006. Efficiency of model-based Bayesian methods for detecting hybrid individuals under different hybridization scenarios and with different numbers of loci. *Molecular Ecology,* 15**,** 63-72.

VELARDE, E., EZCURRA, E., HORN, M. H. & PATTON, R. T. 2015. Warm oceanographic anomalies and fishing pressure drive seabird nesting north. *Science Advances,* 1**,** e1400210.

VENABLES, W. & RIPLEY, B. 2003. Modern Applied Statistics with S. JSTOR.

WAGGITT, J. J., BRIFFA, M., GRECIAN, W. J., NEWTON, J., PATRICK, S. C., STAUSS, C. & VOTIER, S. C. 2014. Testing for sub-colony variation in seabird foraging behaviour: ecological and methodological consequences for understanding colonial living. *Marine Ecology Progress Series,* 498**,** 275-285.

WAKEFIELD, E. D., BODEY, T. W., BEARHOP, S., BLACKBURN, J., COLHOUN, K., DAVIES, R., DWYER, R. G., GREEN, J., GRÉMILLET, D., JACKSON, A. L., JESSOPP, M. J., KANE, A., LANGSTON, R. H. W., LESCROËL, A., MURRAY, S., LE NUZ, M., PATRICK, S. C., PÉRON, C., SOANES, L., WANLESS, S., VOTIER, S. C. & HAMER, K. C. 2013. Space Partitioning Without Territoriality in Gannets. *Science*.

WALTHER, G.-R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J.-M., HOEGH-GULDBERG, O. & BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature,* 416**,** 389-395.

WARWICK-EVANS, V., ATKINSON, P. W., ARNOULD, J. P. Y., GAUVAIN, R., SOANES, L., ROBINSON, L. A. & GREEN, J. A. 2016. Changes in behaviour drive inter-annual variability in the at-sea distribution of northern gannets. *Marine Biology,* 163**,** 1-15.

WEIMERSKIRCH, H. 2007. Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography,* 54**,** 211-223.

WEIMERSKIRCH, H., CHEREL, Y., DELORD, K., JAEGER, A., PATRICK, S. C. & RIOTTE-LAMBERT, L. 2014. Lifetime foraging patterns of the wandering

albatross: Life on the move! *Journal of Experimental Marine Biology and Ecology,* 450**,** 68-78.

WEIMERSKIRCH, H., CORRE, M. L., ROPERT-COUDERT, Y., KATO, A. & MARSAC, F. 2006a. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. *Oecologia,* 146**,** 681-691.

WEIMERSKIRCH, H., DELORD, K., GUITTEAUD, A., PHILLIPS, R. A. & PINET, P. 2015. Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. *Sci Rep,* 5**,** 8853.

WEIMERSKIRCH, H., GAULT, A. & CHEREL, Y. 2005c. Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology,* 86**,** 2611-2622.

WEIMERSKIRCH, H., LE CORRE, M., JAQUEMET, S. & MARSAC, F. 2005b. Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Marine Ecology Progress Series,* 288**,** 251-261.

WEIMERSKIRCH, H., LE CORRE, M., SÃƒ Â©BASTIEN, J., MICHEL, P. & FRANCIS, M. 2004. Foraging strategy of a top predator in tropical waters: great frigatebirds in the Mozambique Channel. *Marine Ecology Progress Series,* 275**,** 297-308.

WEIMERSKIRCH, H., LOUZAO, M., DE GRISSAC, S. & DELORD, K. 2012. Changes in Wind Pattern Alter Albatross Distribution and Life-History Traits. *Science,* 335**,** 211-214.

WEIMERSKIRCH, H., SALAMOLARD, M., SARRAZIN, F. & JOUVENTIN, P. 1993. Foraging Strategy of Wandering Albatrosses through the Breeding Season: A Study Using Satellite Telemetry. *The Auk,* 110**,** 325-342.

WEIMERSKIRCH, H., SHAFFER, S. A., TREMBLAY, Y., COSTA, D. P., GADENNE, H., KATO, A., ROPERT-COUDERT, Y., SATO, K. & AURIOLES, D. 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Marine Ecology Progress Series,* 391**,** 267-278.

WEIMERSKIRCH, H., ZIMMERMANN, L. & PRINCE, P. A. 2001. Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behavioral Ecology,* 12**,** 22-30.

WELCH, A. J. 2011. *Conservation Genetics of the Endangered Hawaiian Petrel (Pterodroma sandwichensis) Across Space and Time.* Doctor of Philosophy, University of Maryland.

WIGGERT, J. D., MURTUGUDDE, R. G. & CHRISTIAN, J. R. 2006. Annual ecosystem variability in the tropical Indian Ocean: Results of a coupled bio-physical ocean general circulation model. *Deep Sea Research Part II: Topical Studies in Oceanography,* 53**,** 644-676.

WILEY, A., WELCH, A., OSTROM, P., JAMES, H., STRICKER, C., FLEISCHER, R., GANDHI, H., ADAMS, J., AINLEY, D., DUVALL, F., HOLMES, N., HU, D., JUDGE, S., PENNIMAN, J. & SWINDLE, K. 2012. Foraging segregation and genetic divergence between geographically proximate colonies of a highly mobile seabird. *Oecologia,* 168**,** 119-130.

WILSON, G. A. & RANNALA, B. 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics,* 163**,** 1177-1191.

WILSON, R. P., DUCAMP, J., REES, W., CULIK, B. & NIEKAMP, K. 1992. Estimation of location: global coverage using light intensity. *Wildlife telemetry: remote monitoring and tracking of animals***,** 131-134.

WINSHIP, A. J., JORGENSEN, S. J., SHAFFER, S. A., JONSEN, I. D., ROBINSON, P. W., COSTA, D. P. & BLOCK, B. A. 2012. State-space framework for estimating measurement error from double-tagging telemetry experiments. *Methods in Ecology and Evolution,* 3**,** 291-302.

WOLF, M. & WEISSING, F. J. 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution,* 27**,** 452-461.

YEN, P. P., SYDEMAN, W. J. & HYRENBACH, K. D. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *Journal of Marine systems,* 50**,** 79-99.

YOUNG, H. S., MAXWELL, S. M., CONNERS, M. G. & SHAFFER, S. A. 2015. Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific. *Biological Conservation,* 181**,** 226-235.

YOUNG, H. S., SHAFFER, S. A., MCCAULEY, D. J., FOLEY, D. G., DIRZO, R. & BLOCK, B. A. 2010. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. *Marine Ecology Progress Series,* 403**,** 291-301.

YOUNG, L. 2010. Inferring colonization history and dispersal patterns of a long-lived seabird by combining genetic and empirical data. *Journal of Zoology,* 281**,** 232-240.

ZINO, F., BROWN, R. & BISCOITO, M. 2008. The separation of Pterodroma madeira (Zino's petrel) from Pterodroma feae (Fea's petrel)(Aves: Procellariidae). *Ibis,* 150**,** 326-334.