ECOLOGY, TAXONOMIC STATUS, AND CONSERVATION OF THE SOUTH GEORGIAN DIVING PETREL (*Pelecanoides georgicus*) IN NEW ZEALAND

BY

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ABSTRACT

ROCELLARIFORMES IS A diverse order of seabirds under considerable pressure from onshore and offshore threats. New Zealand hosts a large and diverse community of Procellariiformes, but many species are at risk of extinction. In this thesis, I aim to provide an overview of threats and conservation actions of New Zealand's Procellariiformes in general, and an assessment of the remaining terrestrial threats to the South Georgian Diving Petrel (Pelecanoides georgicus; SGDP), a Nationally Critical Procellariiform species restricted to Codfish Island (Whenua Hou), post invasive species eradication efforts in particular. I reviewed 145 references and assessed 14 current threats and 13 conservation actions of New Zealand's Procellariiformes (n = 48) in a meta-analysis. I then assessed the terrestrial threats to the SGDP by analysing the influence of five physical, three competition, and three plant variables on nest-site selection using an information theoretic approach. Furthermore, I assessed the impacts of interspecific interactions at 20 SGDP burrows using remote cameras. Finally, to address species limits within the SGDP complex, I measured phenotypic differences (10 biometric and eight plumage characters) in 80 live birds and 53 study skins, as conservation prioritisation relies on accurate taxonomic classification. The results from the meta-analysis revealed that New Zealand's Procellariiformes are at risk from various threats ($\bar{x} = 5.50 \pm 0.34$), but species also receive aid from several conservation actions (\bar{x} = 7.19 ± 0.33). Results from a logistic regression showed that smaller species are more threatened onshore than offshore. The majority of the conservation actions appear in place where needed. However, habitat management, native predator control and the mitigation of risks associated with environmental stochasticity may need improvement. Analysis of SGDP nest-site selection showed dependency on mobile, steep, seaward-facing foredunes. Invasive plant species, the presence of conspecifics, or the presence of other seabird species did not influence SGDP nest-site selection. Assessment of interspecific interactions at SGDP burrows showed seven species occurring at burrows, but only Common Diving Petrels (P. urinatrix; CDP) interfered with SGDP breeding success. Assessment of phenotypic differences within the SGDP revealed that the New Zealand SGDP population differs in five biometric and three plumage

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characters from all other populations and warrants species status based on a species delimitation test with quantitative criteria. I propose to name this Critically Endangered species *Pelecanoides taylorii sp. nov.* These findings indicate that *P. taylorii* is of considerable conservation concern and additional measures, even after successful eradication of invasive species, may be required to safeguard this species. Based on the habitat preference, stochastic events, such as storms and storm surges, appear a major threat to *P. taylorii.* The assessed interspecific interactions at nest-sites, indicate competition with CDPs to be a minor threat. I propose a translocation as a potential strategy to relieve the pressure on *P. taylorii*, but further monitoring and research is needed to enable the implementation of such a conservation strategy.

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PERMITS

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ACRONYMS

AICc	Akaike Information Criterion, corrected for small sample sizes
AIR	Active Infrared
AMNH	American Museum of Natural History, New York, U.S.A.
ANOVA	Analysis of Variance
BMNH	Natural History Museum, Tring, U.K.
CDP	Common Diving Petrel (Pelecanoides urinatrix)
DOC	New Zealand Department of Conservation
GLM	Generalised Linear Model
IUCN	International Union for Conservation of Nature
LM	Linear Model
LOESS	Locally Estimated Scatterplot Smoothers
MCA	Multiple Correspondence Analysis
NMNZ	Te Papa Tongarewa Museum of New Zealand, Wellington, New Zealand
PCA	Principal Component Analysis
PIR	Passive Infrared
RFID	Radio Frequency Identification
RVI	Relative variable importance
SAO	South Atlantic Ocean
SGDP	South Georgian Diving Petrel (Pelecanoides georgicus)
SIO	Southern Indian Ocean
SPO	South Pacific Ocean

Chapter 1

Chapter 1. GENERAL INTRODUCTION

CONSERVATION BIOLOGY IS the science aimed at countering the human-induced, cataclysmic mass-extinction. Anthropogenic changes to the environment have had unprecedented impacts on the biosphere, resulting in extinction rates 100 to 1000 times higher than pre-human rates (Pimm *et al.* 1995, Hoffmann *et al.* 2010). These human-induced changes are not only apparent on a global scale, but also occur within a relatively small timeframe (Pimm *et al.* 1995). Numerous species are on the brink of extinction due to these wide-ranging, rapid changes. The IUCN (2016) lists 4749 species that are at extremely high risk (i.e. Critically Endangered), 7050 species at very high risk (i.e. Endangered) and 10,694 species at high risk (i.e. Vulnerable) of extinction. Conservation biology aims to prevent the extinction of these and other species, and while extinction rates are increasing, conservation efforts are slowing the rate of increase (Hoffman *et al.* 2010). However, given the vast number of threatened species and the limited resources at hand, conservation prioritisation is challenging (Brooks *et al.* 2006).

Procellariiformes is a severely threatened order of seabirds, whose members are ecosystem engineers – species with a disproportionate influence on the surrounding environment – and thus of high conservation interest. The order Procellariiformes is diverse and encompasses approx. 100 seabird species, including some of the largest (Albatrosses) and some of the smallest seabird species (e.g., Storm Petrels) (Marchant & Higgins 1990, Gill *et al.* 2010). Procellariiform species are distributed throughout the world's oceans, but most species occur in the southern hemisphere (Marchant & Higgins 1990). Procellariiformes is one of the most threatened bird orders (Butchart *et al.* 2004, Croxall *et al.* 2012) and the life history traits of these species (slow population growth rates, small clutch sizes, and long incubation and chick rearing stage; *K*-strategy) render these species particularly prone to extinctions (Duncan & Blackburn 2004, Satterthwaite & Mangel 2012). Consequently, a substantial percentage (43 %) of Procellariiform species is currently threatened with extinction (IUCN 2016). Some of these species rank among the rarest and most threatened birds in the world, as 12 species are listed as Critically

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Endangered. This is of major conservation concern, as Procellariiformes enable nutrient cycling between terrestrial and pelagic ecosystems, alter soil properties through bioturbation, and influence the vegetation in their breeding colonies. (Sekercioglu *et al.* 2004, Hawke & Holdaway 2005, Paleczny *et al.* 2015). The presence of these birds also enhances the diversity of invertebrates and reptiles (Markwell & Daugherty 2002). Furthermore, these birds act as seed dispersers (Falla 1960, Cheke & Hume 2010). Moreover, Procellariiformes are considered indicators of various ecosystem changes because of their placement on high trophic levels, large ranges and long lifespans (Furness & Camphuysen 1997, Paleczny *et al.* 2015).

New Zealand is of global conservation importance to Procellariiformes. New Zealand hosts one of the most diverse communities and the highest number of endemic species of Procellariiform of any country (Taylor 2000, Croxall et al. 2012). Currently four families encompassing 48 different Procellariiform species breed within the boundaries of New Zealand, of which 18 are endemic to the area (Taylor 2000, Gill *et al.* 2010). Another approximately 30 species visit New Zealand's waters as passage migrant, winter visitor or vagrant (Gill et al. 2010, Heather & Robertson 2015). Procellariiform species in New Zealand have suffered significant population declines due to anthropogenic influences (Taylor 2000) and at least two species have been extirpated following human settlement (Tennyson et al. 2015). Various methods are used to conserve New Zealand's Procellariiform species (e.g., Miskelly et al. 2009, Gummer et al. 2015, Jones et al. 2016). Yet most species are still under considerable pressure from both onshore and offshore threats (Taylor 2000) and 18 species breeding in New Zealand are considered at direct risk of extinction (IUCN 2016). The New Zealand Department of Conservation (DOC) also maintains a national threat ranking system and this ranks 11 Procellariiform species as Nationally Critical, Nationally Endangered or Nationally Vulnerable (Robertson et al. 2013).

Caughley (1994) identified two paradigms within conservation biology: the small and the declining population paradigm. The first is involved with identifying and mitigating the negative effects caused by the small size of a population (e.g., inbreeding or stochasticity). The second is concerned with the causes of the population decline (e.g., overkill or habitat loss). Invasive species also fall under the declining population paradigm (Caughley 1994) and are part of Diamond's (1984) "evil quartet" of extinction drivers. Predation by invasive species represents one of

the main causes of Procellariiform population declines in New Zealand (Taylor 2000). New Zealand has successfully eradicated invasive species on increasingly large islands (Towns & Broome 2003, Jones *et al.* 2016). Such eradications had a variety of beneficial outcomes for Procellariiformes, including the release of habitat constraints and population increases (Taylor 2000, Middleton 2007, Rayner *et al.* 2008, Buxton *et al.* 2015, Jones *et al.* 2016). However, other threats, besides invasive species, within both the small and the declining population paradigm, may also imperil New Zealand's Procellariiformes (Taylor 2000).

An example of a highly threatened Procellariiform taxon in New Zealand is the South Georgian Diving Petrel (Pelecanoides georgicus; SGDP). This small species (90-160 g; Taylor & Cole 2002) has a wide distribution across the southern oceans and is considered Least Concern by the IUCN (2016). The SGDP was also widespread and numerous in southern New Zealand (Figure 1), but the species has been affected by local extinctions throughout the majority of its historic range and the species was extirpated on the Auckland Islands (Dundas and Enderby Island), Chatham Islands, Stewart Island (Mason Bay) and the Otago Peninsula (Sandfly Bay) (Marchant & Higgins 1990, Worthy 1998, Taylor 2000, Holdaway et al. 2003, Wood & Briden 2008). The last remaining SGDP population in New Zealand persists in the Sealers Bay dunes of Codfish Island (Whenua Hou) and numbers approximately 150 individuals only (Wood & Briden 2008, Taylor 2013). This precarious state has resulted in the species being listed as Nationally Critical (Robertson *et al.* 2013). Invasive species have been eradicated from Codfish Island, partly to aid the various Procellariiform populations present on the island (Middleton 2007). No distinct population increase has been observed for the SGDP population post eradication efforts (Taylor 2000, Wood & Briden 2008, Taylor 2013), which contrasts with the responses observed in other Procellariiform species present on the island (Middleton 2007, Rayner et al. 2008). Consequently, other inhibiting factors may be limiting the SGDP population on Codfish Island. Various threats have been hypothesised, including the encroachment of the Sealers Bay dunes (Taylor 2013), erosion caused by stochastic events and catastrophes (Cole 2004), predation by Moreporks (*Ninox novaeseelandiae*) (Trainor 2008) and competition with Common Diving Petrels (*P. urinatrix*; CDP) for nest-sites (Taylor & Cole 2002). No offshore threats affecting the SGDP are currently recognised, but collision with ships has been reported at other colonies (Black 2005). Moreover,

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the SGDP population on Codfish Island might be the last population of an undescribed species (Paterson *et al.* 2000). Consequently, the last remaining SGDP population in New Zealand may be of considerable global conservation concern.

The objective of this study is to provide further insights on the threats and conservation of New Zealand's Procellariiformes in general, and the ecology, current risks and taxonomic status of the SGDP in New Zealand in particular. In Chapter 2, I present a meta-analysis investigating the current threats and conservation actions of New Zealand's Procellariiformes. In Chapter 3, I analyse the nest-site selection of the SGDP on Codfish Island and infer terrestrial threats to the population. In Chapter 4, I assess interspecific interactions at SGDP burrows and their effects on SGDP breeding success with remote cameras. In addition, I assess the utility of remote cameras for breeding biology studies. In Chapter 5, I analyse phenotypic differences between SGDP populations and assess the taxonomic status of the Codfish Island SGDP population. I use the results presented in these chapters to discuss the potential directions for future conservation management in order to reinstate population growth, and ultimately, securing the SGDP population in New Zealand (Chapter 6).



Figure 1. Historic and present distribution of the South Georgian Diving Petrel in southern New Zealand (including Macquarie Island, Australia).

Chapter 2

Chapter 2. A META-ANALYSIS OF CURRENT THREATS AND CONSERVATION ACTIONS OF PROCELLARIIFORMES IN NEW ZEALAND

ABSTRACT

LARGE PORTION of the world's Procellariiformes breeds in New Zealand and A many of these are threatened with extinction. As these species are faced with an array of threats that occur in different ecosystems, implementation of conservation management can be challenging. To provide an overview and to inform management, I assessed current threats and conservation actions of New Zealand's Procellariiform species (families Diomedeidae, Procellariidae, Hydrobatidae and Pelecanoididae; n = 48). I reviewed 145 relevant references and constructed presence/absence databases of 14 threats and 13 conservation actions. Using these databases as a foundation for a meta-analysis, I showed that several threats imperil individual species (\bar{x} = 5.50 ± 0.34), but species also benefited from a range of conservation actions (\bar{x} = 7.19 ± 0.33). Invasive species (n = 42 affected species), line fisheries (n = 36) and net fisheries (n = 4235) are the most commonly recognized threats. The most common conservation actions are bycatch management (n = 48), population census/survey (n = 48) and research investigating population dynamics and breeding biology (n = 46). Results of a logistic regression (GLM) illustrate that larger species are more likely to be threatened offshore, while smaller species are more often threatened onshore $(R^{2}_{McFadden} = 0.254)$. In addition, I used Fisher's exact tests, Spearman correlation tests and multiple correspondence analyses (MCA) to test for correlation and correspondence between certain threats and conservation actions. These reveal that the majority of conservation actions are in place where needed. Improvements could be made in addressing negative effects caused by native predators (p = 0.354) and environmental stochasticity (p = 0.214), and potentially habitat loss. While the qualitative meta-analysis presented here provides a broad overview for New Zealand's Procellariiformes, further monitoring and research is needed to assess the quantitative effects of threats and conservation actions.

INTRODUCTION

Seabirds have a relatively low diversity (approx. 350 species) compared to other species groups (e.g., songbirds with approx. 5000 species) (Croxall *et al.* 2012, Moyle *et al.* 2016). Despite this low diversity, seabirds have attracted a considerable amount of attention on a global scale (Croxall *et al.* 2012). A possible explanation for this interest in seabirds may be that they are considered reliable indicators of ecosystem changes on large temporal and geographical scales, because most species are wide-ranging, long-lived, and placed on high trophic levels (Furness & Camphuysen 1997, Paleczny *et al.* 2015). In addition, seabirds fulfil important ecosystem functions, as they can act as ecosystem engineers and increase nutrient cycling between ecosystems (Sekercioglu *et al.* 2004, Paleczny *et al.* 2015). The presence of seabirds also boosts the diversity of other species groups (Markwell & Daugherty 2002). Unfortunately, Paleczny *et al.* (2015) showed that seabird populations suffered a global decrease of 70% in the last 60 years and consequently, many seabird species are currently threatened with extinction (IUCN 2016).

Seabirds spend most of their time foraging at sea, but return to land to breed and, for some species, to roost, and thus they are influenced by a variety of onshore and offshore threats. One of the main perils at sea is the accidental bycatch by commercial longline and trawl fisheries, which causes the death of several 100,000 seabirds each year (Tuck *et al.* 2003, Abraham & Thompson 2011, Maree *et al.* 2014, Rollinson *et al.* 2014). In addition, ingestion of plastic debris (Fry *et al.* 1987, Wilcox *et al.* 2015) and contamination with chemical pollutants (Furness & Camphuysen 1997, Chu *et al.* 2015) have been identified as offshore threats to many seabird species. A prevalent terrestrial threat to seabirds is predation of eggs, chicks and, sometimes, adults, by invasive mammalian species such as rats (*Rattus* ssp.) (Jones *et al.* 2007) or cats (*Felis catus*) (Keitt *et al.* 2002). Much effort has been invested to eradicate such problematic species (e.g., Towns & Broome 2003, Phillips 2010, Jones *et al.* 2016). Furthermore, seabirds are also threatened onshore by the loss of suitable nesting habitat (Croxall *et al.* 2012) and human disturbance (Higham 1998) among others.

New Zealand contains the one of the most diverse seabird communities in the world (Taylor 2000) and was listed by Croxall *et al.* (2012) as the most threatened

community in the world. Furthermore, New Zealand hosts the highest number of endemic seabird species (n = 35) in the world (Taylor 2000, Croxall *et al.* 2012). The majority (58%) of New Zealand's seabird species belong to the order Procellariiformes (Gill *et al.* 2010, Heather & Robertson 2015). Many Procellariiformes are currently threatened with extinction. The IUCN (2016) has ranked 12 species as Critically Endangered, 18 as Endangered and 30 as Vulnerable. A considerable proportion of these threatened species breeds in New Zealand (2, 3, and 13, respectively). The New Zealand Department of Conservation (DOC) also maintains a national threat classification system (Robertson *et al.* 2013). In this system five Procellariiformes were ranked as Nationally Critical, two as Nationally Endangered and four as Nationally Vulnerable. Both threat classification systems underline the importance of New Zealand for Procellariiformes and the need for their conservation.

Given the array of potential threats, directing conservation management to secure and protect Procellariiformes can be challenging. Many studies have focused on the effects of a single threat or conservation action for a single species (e.g., Bell *et al.* 2005, Keitt *et al.* 2006) and several studies have directed their attention towards patterns across several species (e.g., Jones *et al.* 2007, Abraham & Thompson 2011). Yet such studies are often limited to threats within a single ecosystem. As Procellariiform species rely on two entirely different ecosystems, broader overviews may be required to ensure conservation actions are directed successfully.

Using a meta-analysis of published references, I provide a qualitative review of the spread and nature of current threats and conservation actions of all Procellariiformes breeding in New Zealand. Specifically, I aim to address the following questions: 1) How are current threats spread among New Zealand's Procellariiformes? 2) What is the relationship between body weight and threats? 3) How are current conservation actions are spread among New Zealand's Procellariiformes? 4) What is the relationship between body weight and the spread of conservation actions? 5) Are conservation actions targeted directly at mitigating particular threats?

METHODS

Study area and species

The geographical scope of this meta-analysis is limited to New Zealand and its marine territories. I defined this area as the mainland of New Zealand including offshore island such as the Kermadec, Chatham, Bounty, Auckland, Campbell and Snares Islands as well as the New Zealand Exclusive Economic Zone (EEZ).

I assessed 48 Procellariiform species, of which 18 are endemic breeders to New Zealand. These 48 species represented four families: Diomedeidae (n = 11), Procellariidae (n = 29), Hydrobatidae (n = 6) and Pelecanoididae (n = 2). I only included Procellariiformes taxa that breed successfully within the study area, following the taxonomy of Gill *et al.* (2010). Therefore, I excluded migrants, wintervisitors, or vagrants to New Zealand, as well as populations that breed outside of New Zealand. For polytypic species, I solely assessed taxa breeding in New Zealand. Furthermore, I limited the taxonomic scope of this study to species level, and thus jointly assessed different subspecies of polytypic species breeding in New Zealand.

Literature review

I used both Google Scholar and Web of Science to search for literature by using the English and scientific name of each of the 48 target species as search term. In addition, I used Taylor (2000), Miskelly (2013) and IUCN (2016) as a starting point for further literature searches to account for relevant grey literature, such as internal DOC reports, that are unlikely to be found through regular search engines. I did not include literature published before 2000 in order to limit the scope of this meta-analysis to current threats and conservation actions. In total, I reviewed 145 references published between 2000 and 2015 as the fundament of this meta-analysis (Appendix 1).

Assessment of threats

Based on the sourced literature, I constructed a presence/absence database with 14 categories of threats faced by New Zealand's Procellariiformes (Appendix 2). I considered seven categories to be onshore threats and five to be offshore threats (Table 1). I considered two additional threat categories to be neither land- nor sea-

based (non-spatial). I also classified the area of the most detrimental threats (onshore/offshore) per species in order to gain a better understanding of the overall patterns in threats. I based this classification of severity on a combination of number of references, data quality and, where necessary, data on closely related species.

Assessment of conservation actions

I also constructed a presence/absence database with 13 conservation action categories to evaluate the spread of current conservation actions directed at New Zealand's Procellariiformes (Appendix 3). I considered six conservation actions to be land-based and five to be sea-based (Table 2). I considered two additional conservation actions to be neither onshore nor offshore actions (non-spatial). Furthermore, I assumed certain conservation action categories to be aimed to mitigate particular threat categories (n = 8).

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Threat category	Area	Definition
Invasive species (IS)	Onshore	Any species that is introduced outside of its native range having a direct, negative impact
		(e.g., rats <i>Rattus ssp</i>).
Native predators (NP)	Onshore	Any species native to New Zealand having a direct negative impact through predation.
Habitat loss (HL)	Onshore	Any negative effect caused by loss of suitable breeding habitat that is not directly caused
		another threat category.
Human disturbance (HD)	Onshore	Any form of land-based human interaction that has a negative impact (e.g., ecotourism,
		investigator disturbance, collision with wires etc.), except for light pollution.
Environmental	Onshore	Stochastic events that have or could have a negative impact on breeding colonies (e.g.,
stochasticity (ES)		fires, floods, storms).
Interspecific competition (C)	Onshore	Competition (e.g., for nest-sites) between two native species having a negative impact.
	-	
Disease and parasites	Unshore	Any form of pathogen that has a negative impact (e.g., avian malaria, avian pox, leeches,
(D.P)		ticks etc.).
Line fisheries (LF)	Offshore	Any negative effect (e.g., accidental bycatch or entanglement) caused by commercial
		(e.g., long-line) or recreational (e.g., reel) fishing lines.
Net fisheries (NF)	Offshore	Any negative impact (e.g., accidental bycatch, entanglement or collision) caused by
		fisheries using nets (including trawl, set, warp, drift, monofilament and gill nets).
Resource competition	Offshore	Any negative effects caused by resource competition between humans and
with humans (RC)		Procellariiformes (e.g., over-fishing).
Marine pollution (MP)	Offshore	Any negative impact caused by some form of marine pollution (e.g., chemicals, plastics
		etc.), except oil spills.
Oil spills (OS)	Offshore	Any negative effect caused by the spilling of (raw) oil into the sea.
Climate change (CC)	I	Any form of negative effect caused by climate change.
Light pollution (LP)	ı	Any negative effects that are attributed to artificial lights at night (e.g., disorientation or

Conservation action category	Area	Definition	Corresponding threat category
Invasive species control (IC)	Onshore	Any action involved with the active removal (e.g., poisoning, trapping,	Invasive species
Native predator control (NPC)	Onshore	Any action involved with the mitigation of negative effects caused by	Native predators
Competition management (CM)	Onshore	Any action involved with the intentional inhibition of inter-specific	Interspecific
		competition between marive species (e.g., by blocking buillow entrances).	compendion
Habitat management (HM)	Onshore	Any restoration or management effort that is directed towards	Habitat loss
Human disturbance management (HDM)	Onshore	Any action involved with the reduction of human disturbance, aperles. from reservation.	Human disturbance
Translocations (T)	Onshore	Any action involved with the reinforcement, reintroduction or assisted colonisation, as defined by Seddon <i>et al.</i> (2014).	Environmental stochasticity
Pelagic distribution mapping	Offshore	Any action involved with the identification and mapping offshore home	
(PDM) Dietary studies (DS)	Offshore	ranges. Any action involved with the identification of dietary requirements	
Duratal according (DA)	Offebaue	(e.g., feeding methods, prey species, or nutritional requirements).	
Dycatch assessment (DA)	OIISIIUE	Any actuol involved with the neutrinearon of negative impacts caused by activities of fisheries.	1
Bycatch management (BM)	Offshore	Any action involved with the mitigation of negative effects caused by commercial or recreational fisheries	Line fisheries and Net fisheries
Marine pollution assessment (PA)	Offshore	Any action involved with the identification of the effects of marine	Marine pollution
Population census/survey (PC.S)	ı	Any action involved in estimating population sizes.	I
Population dynamics and	ı	Any action addressing population trends and describing the breeding	
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Table 2. Categories of conservation actions (and acronyms) directed towards New Zealand's Procellariiformes.

Data analysis

I used the databases (Appendix 2 & 3) to assess patterns of threats and conservation actions of New Zealand's Procellariiformes. I analysed the differences in number of threats and conservation actions between families and endemics and non-endemics using factorial ANOVAs and Welch two-sample t-test, respectively. I excluded Pelecanoididae from these statistical analyses due to the low sample size (n = 2).

I analysed the relationship between body weight (g) and the number of threats, whether the most detrimental threats occurred onshore or offshore (main area of threats), and the number of conservation actions. For this, I sourced body weight data for each species from Scofield & Stephenson (2013), del Hoyo *et al.* (2015) and Heather & Robertson (2015). I then calculated the midpoint between the minimum and the maximum weight of each species. I calculated the midpoint as an approximation of the mean, because weight data of similar quality were not available for each species and I assumed that weight variation within species followed normal distribution. I then assessed the relationship between body weight and the main area of threats using a generalized linear model (GLM) with body weight as the independent and main area of threats as the dependent variable. I also assessed the relationship between the number of threats and conservation actions per species and body weight using linear models (LM).

I assumed that certain conservation action categories were directly aimed at the mitigation of certain threat categories. I therefore analysed how well these conservation action categories corresponded and correlated with their respective threat categories. First, I used Spearman correlation tests to assess correlation between threat and conservation action categories. Then I constructed contingency tables (based on presence/absence) and subsequently analysed these using Fisher's exact tests. I assumed bycatch management to aid all target species and thus this variable became a constant. Therefore, I excluded this variable from analyses with Fisher's exact tests and Spearman correlation tests. Finally, I performed two multiple correspondence analyses (MCA) to reduce dimensionality of variables and factors: one for onshore and one for offshore threats and conservation actions. I included nonspatial threats and conservation actions in both MCAs. I conducted all analyses in Program R (R Development Core Team 2016) using the Hmisc (Harrel 2016), the FactoMineR (Le *et al.* 2008) and the ggplot2 packages (Wickham 2009).

RESULTS

Threats

Threats that affect the most species of New Zealand's Procellariiformes are: invasive species (n = 42 affected species), line fisheries (n = 36), net fisheries (n = 35), environmental stochasticity (n = 30) and human disturbance (n = 29) (Figure 2). On average, species are threatened by 5.50 ± 0.34 different threats, of which 3.13 ± 0.20 are onshore, 1.94 ± 0.20 are offshore and 0.44 ± 0.08 are non-spatial threats (Table 3). The number of threats does not differ among Procellariiformes families overall ($f_{2,43} = 0.928$, p = 0.403), onshore ($f_{2,43} = 0.100$, p = 0.905) or offshore ($f_{2,43} = 2.409$, p = 0.102). Endemics and non-endemics also do not face significantly different number of threats overall (t = -1.148, df = 37.137, p = 0.259), onshore (t = -0.866, df = 45.007, p = 0.391) or offshore (t = -1.297, df = 29.948, p = 0.243).

The assessment of main area of threats shows that 32 species are primarily threatened by onshore threats, while 16 species were primarily threatened by offshore threats. The main area of threats has a very strong relationship with body weight (R^2 _{McFadden} = 0.254) (R^2 _{McFadden} = 0.2-0.4 indicates excellent fit; Domencich & McFadden 1975). With increasing body weight, the area of the most important threats shifts from onshore to offshore (Figure 3). Body weight of species is not related to the number of threats overall (R^2 = 0.045, p = 0.147), onshore (R^2 = 0.010, p = 0.502) or offshore (R^2 = 0.061, p = 0.091).



Figure 2. Number of New Zealand's Procellariiform species per threat and conservation action category. Threat acronyms: IS = invasive species, ES = environmental stochasticity, HD = human disturbance, HL = habitat loss, C = interspecific competition, D.P = disease and parasites, LF = line fisheries, NF = net fisheries, MP = marine pollution, OS = oil spills, LP = light pollution, CC = climate assessment, DS = dietary studies, PDM = pelagic distribution mapping, PA = marine pollution assessment, PS.C = population change. Conservation action acronyms: IC = invasive species control, T = translocations, HDM = human disturbance management, CM = competition management, HM = habitat management, NPC = native predator control, BM = bycatch management, BA = bycatch Onshore Offshore Non-spatial survey/census, PD = population dynamics and breeding biology research.

Area

Table 3. Mean ± standard	l error of mean (minimum-ma	ximum) number of threats	affecting, and conservation a	actions directed towards
New Zealand's Procellar	iiformes. Differences of mea	ns were analysed using fa	actorial ANOVAs (Diomedei	idae, Procellariidae and
Hydrobatidae) and Welch	1 two-sample t-tests (endemi	s/non-endemics). Pelecanc	vididae was excluded from s	tatistical analyses due to
low sample size. * indicat	es $p < 0.05$, ** indicates $p < 0$.	01 and *** indicates $p < 0.0$	01.	
Threats	All	Onshore	Offshore	Non-spatial
All species (n = 48)	5.50 ± 0.34 (0-10)	3.13 ± 0.20 (0-6)	$1.94 \pm 0.20 \ (0-5)$	0.44 ± 0.08 (0-2)
Diomedeidae (n = 11)	6.18 ± 0.50 (4-8)	$3.18 \pm 0.40 (1-5)$	2.55 ± 0.16 (2-3)	$0.46 \pm 0.16 (0-1)$
Procellariidae (n = 29)	5.28 ± 0.47 (0-10)	2.97 ± 0.26 (0-5)	$1.93 \pm 0.27 (0-5)$	0.38 ± 0.12 (0-2)
Hydrobatidae (n = 6)	4.67 ± 1.02 (2-8)	3.00 ± 0.52 (2-5)	$1.17 \pm 0.40 (0-2)$	0.50 ± 0.22 (0-2)
Pelecanoididae (n =2)	7.50 ± 1.50 (6-9)	$5.50 \pm 0.50 (5-6)$	$1.00 \pm 1.00 (0-2)$	$1.00 \pm 0.00 (1-1)$
Endemics (n = 18)	6.00 ± 0.54 (2-10)	3.33 ± 0.26 (2-5)	2.28 ± 0.34 (0-5)	$0.39 \pm 0.14 (0-2)$
Non-endemics (n = 30)	5.20 ± 0.45 (0-9)	3.00 ± 0.29 (0-6)	1.80 ± 0.22 (0-4)	0.40 ± 0.10 (0-2)
Conservation actions				
All species (n = 48)	7.19 ± 0.22 (2-10)	$1.63 \pm 0.13 (0-4)$	$3.60 \pm 0.15 (1-5)$	1.96 ± 0.03 (1-2)
Diomedeidae (n = 11)	7.64 ± 0.31 (6-9)	$1.45 \pm 0.25 (0-3)$	4.18 ± 0.18 (3-5)	2.00 ± 0.00 (2-2)
Procellariidae (n = 29)	7.28 ± 0.32 (2-10)	$1.72 \pm 0.19 (0-4)$	$3.59 \pm 0.19 (1-5)$	$1.97 \pm 0.03 (1-2)$
Hydrobatidae (n = 6)	6.17 ± 0.48 (5-8)	$1.17 \pm 0.17 (1-2)$	3.17 ± 0.31 (2-4)	$1.83 \pm 0.17 (1-2)$
Pelecanoididae (n = 2)	6.50±50 (6-7)	2.50 ± 0.50 (2-3)	$2.00 \pm 1.00 (1-3)$	2.00 ± 0.00 (2-2)
Endemics (n = 18)	7.83 ± 0.29 (5-10) *	$1.89 \pm 0.20 (1-4)$	$4.00 \pm 0.20 (2-5) *$	$1.94 \pm 0.06 (1-2)$
Non-endemics (n = 30)	$6.84 \pm 0.29 (2-10) *$	1.48 ± 0.17 (0-4)	$3.39 \pm 0.19 (1-5) *$	$1.97 \pm 0.03 (1-2)$

Procellariiformes Threats & Conservation actions



Figure 3. The relationship between the main area of threats (1 = onshore, 0 = offshore) to New Zealand's Procellariiformes compared to the body weight (g) of each species, assessed with a general linear model (GLM) including 95% confidence intervals.

Conservation actions

The most common conservation actions undertaken in New Zealand to aid Procellariiformes are bycatch management (n = 48 species), population census/ survey (n = 48), population dynamics and breeding biology research (n = 46), bycatch assessment (n = 44) and invasive species control (n = 43) (Figure 2). On average, species receive 7.19 ± 0.22 different conservation actions, of which 1.63 ± 0.13 are onshore, 3.60 ± 0.15 are offshore and 1.93 ± 0.03 are non-spatial actions (Table 3). The number of actions does not differ between Procellariiformes families overall ($f_{2,43}$ = 1.803, p = 0.177), onshore ($f_{2,43}$ = 1.094 p = 0.344) or offshore ($f_{2,43}$ = 2.788, p = 0.070). Endemic species receive attention from more conservation actions than non-endemics overall (t = -2.484, df = 42.788, p = 0.017) and offshore (t = -2.316, df = 41.718 p = 0.026), but the amount of actions did not differ onshore (t = -1.622, df = 39.349, p = 0.113).

Body weight of species is not related to the number of actions overall ($R^2 = 0.051$, p = 0.124) or actions onshore ($R^2 < 0.001$, p = 0.952). However, body weight has a very weak influence on the number of actions offshore ($R^2 = 0.099$, p = 0.030).

Conservation correspondence

Eight conservation action categories were assumed to be directly aimed at a certain threat category. The majority of these actions are corresponding and correlating significantly with their respective threats (Table 4). However, native predator control and translocations are not significantly corresponding and correlating with their respective threats.

Table 4. Correspondence and correlation between threats affecting New Zealand's Procellariiform species and the mitigating conservation actions assessed by Fisher's exact Tests and Spearman correlation tests. Blank indicates p > 0.05, * indicates p < 0.05, ** indicates p < 0.01 and *** indicates p < 0.001.

Threat	Conservation action	Fisher's exact test	Spearman's r
Invasive species	Invasive species control	***	1.00***
Native predators	Native predator control		0.20
Habitat loss	Habitat management	*	0.38**
Human	Human disturbance	*	0.34*
disturbance	management		
Environmental	Translocations		0.21
stochasticity			
Interspecific	Competition	**	0.54***
competition	management		
Marine pollution	Pollution assessment	***	0.77***

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Results from MCA analyses reveal that both onshore and offshore conservation actions are generally applied where these are needed (Figure 4 & 5, Table 5 & 6). The MCA for onshore threats and conservation actions also shows that there is a distance between interspecific competition and competition management, habitat loss and habitat management, and environmental stochasticity. Furthermore, species suffering from climate change, species for which native predator control is in place, and species without population dynamics and breeding biology research, form outliers. The MCA for offshore threats and conservation actions shows a wider spread than the onshore MCA. The offshore MCA also reveals several outlying groups: 1) species that suffer from resource competition, climate change and light pollution, 2) species that are threatened by oil spills and marine pollution and for which pollution assessment is scored, and 3) species that are not threatened by line fisheries, net fisheries and for which population dynamics and breeding biology studies, dietary studies and bycatch assessment are not scored.

Table 5. Contributions of variables and factors to the 1^{st} and 2^{nd}
dimensions (Dim) of the multiple correspondence analysis (MCA)
of onshore threats and conservation actions of New Zealand's
Procellariiformes (Figure 4).

Variable	Factor	Dim 1	Dim 2
Invasive species (IS)	Absent (_N)	8.573	2.696
	Present (_Y)	1.225	0.385
Native predators (NP)	Absent (_N)	0.378	4.314
	Present (_Y)	0.689	7.866
Habitat loss (HL)	Absent (_N)	4.360	0.382
	Present (_Y)	9.592	0.839
Human disturbance (HD)	Absent (_N)	8.817	1.527
	Present (_Y)	5.777	1.000
Environmental stochasticity (ES)	Absent (_N)	5.302	0.005
	Present (_Y)	3.181	0.003
Interspecific competition (C)	Absent (_N)	0.945	2.287
	Present (_Y)	4.093	9.910
Disease and parasites (D.P)	Absent (_N)	0.001	0.564
	Present (_Y)	0.005	2.821
Light pollution (LP)	Absent (_N)	0.995	0.045
	Present (_Y)	3.781	0.173
Climate change (CC)	Absent (_N)	0.081	3.678
	Present (_Y)	0.351	15.937
Population survey/census (PS.C)	Present (_Y)	0.000	0.000
Population dynamics and breeding biology	Absent (_N)	2.790	9.561
research (PD)	Present (_Y)	0.121	0.416
Invasive species control (IC)	Absent (_N)	7.135	2.868
	Present (_Y)	0.830	0.333
Native predator control (NPC)	Absent (_N)	0.006	0.207
	Present (_Y)	0.299	9.709
Competition management (CM)	Absent (_N)	0.619	0.419
	Present (_Y)	9.287	6.283
Habitat management (HD)	Absent (_N)	0.528	0.014
	Present (_Y)	7.921	0.211
Human disturbance management (HDM)	Absent (_N)	0.483	1.774
	Present (_Y)	1.625	5.966
Translocations (T)	Absent (_N)	3.616	2.765
	Present (_Y)	6.594	5.043

Table 6. Contributions of variables and factors to the 1st and 2nd dimensions (Dim) of the multiple correspondence analysis (MCA) of offshore threats and conservation actions of New Zealand's Procellariiformes (Figure 5).

Variable	Factor	Dim 1	Dim 2
Line fisheries (LF)	Absent (_N)	13.017	1.673
	Present (_Y)	3.870	0.498
Net Fisheries (NF)	Absent (_N)	12.262	0.951
	Present (_Y)	4.554	0.353
Resource competition (RC)	Absent (_N)	0.929	0.514
	Present (_Y)	4.025	2.226
Marine pollution (MP)	Absent (_N)	0.767	4.231
	Present (_Y)	3.833	21.157
Oil spills (OS)	Absent (_N)	0.482	0.919
	Present (_Y)	4.148	7.901
Light pollution (LP)	Absent (_N)	0.205	2.589
	Present (_Y)	0.778	9.839
Climate change (CC)	Absent (_N)	0.720	1.314
	Present (_Y)	3.120	5.693
Population survey/census (PS.C)	Present (_Y)	0.000	0.000
Population dynamics and breeding	Absent (_N)	6.850	1.778
biology research (PD)	Present (_Y)	0.298	0.077
Pelagic distribution mapping (PDM)	Absent (_N)	3.591	2.043
	Present (_Y)	1.795	1.021
Dietary studies (DS)	Absent (_N)	13.037	1.248
	Present (_Y)	1.862	0.178
Bycatch assessment (BA)	Absent (_N)	11.881	1.607
	Present (_Y)	1.080	0.146
Bycatch management (BM)	Present (_Y)	0.000	0.000
Pollution assessment (PA)	Absent (_N)	1.006	4.673
	Present (_Y)	5.890	27.370





invasive species control, IS = invasive species, LP = light pollution, NP = native predators, NPC = native predator control, PD = breeding biology and population research, PS.C = population survey/census, T = translocations. _Y = threat/conservation action present, _N = C = interspecific competition, CC = climate change, CM = competition management, D.P = disease and parasites, ES = environmental stochasticity, HD = human disturbance, HDM = human disturbance management, HL = habitat loss, HM = habitat management, IC = Figure 4. Multiple correspondence analysis (MCA) plot of onshore threats and conservation actions of New Zealand's Procellariiformes. threat/conservation action absent




DISCUSSION

The results of this study show that New Zealand's Procellariiformes are threatened by a range of threats in both terrestrial and pelagic ecosystems. Larger (heavier) species are more threatened by offshore threats, while smaller (lighter) species are mostly threatened by onshore threats. However, body weight has no influence on the amount of threats faced by a species. In addition, a considerable suite of conservation actions is present to mitigate threats. Body weight does not explain the amount of conservation actions per species. In general, these conservation actions appear to be applied where needed, although some gaps exist. Specifically, there appears to be room for improvement to mitigate the risks associated with environmental stochasticity, habitat loss and native predators.

Threats appear spread evenly among New Zealand's Procellariiformes, as neither Procellariiform family, nor endemism, nor body weight influences the number of threats. Procellariiform species are threatened by a larger variety of threats onshore than offshore, but this may be caused by the larger amount of assessed onshore threats than offshore threats.

The shift of main area of threats from terrestrial to pelagic ecosystems with increasing body weight is most likely explained by a lower sensitivity to invasive predators by larger (heavier) Procellariiformes (Jones *et al.* 2007). Larger seabirds such as members of Diomedeidae and *Procellaria* petrels within Procellariidae are less prone to predation by invasive species, but suffer significantly from accidental bycatch at sea (Taylor 2000, Abraham & Thompson 2011).

The demonstrated spread of conservation actions fits international conservation policy. Procellariiform species endemic to New Zealand receive aid from a larger variety of actions than non-endemics, while there is no demonstrated difference between Procellariiform families. New Zealand has the highest number of endemic Procellariiformes (Taylor 2000, Croxall *et al.* 2012) and endemism is seen as an important factor for prioritisation assessments (Myers *et al.* 2000). Therefore, when considering the variety of actions as a proxy for conservation focus, the increased focus on endemics fits well within global conservation prioritisation.

The lack of influence of body weight on the number of conservation actions may be indicative of actions being applied were necessary. In general, larger (and thus

heavier) species are considered more charismatic (Entwistle & Dusntone 2000). Such species are often used as flagship-species, with the reasoning that if these species benefit from conservation management, other, less charismatic species may benefit too. In this meta-analysis of New Zealand's Procellariiforms, however, the flag-ship species conservation approach does not become evident when considering the spread of actions as a proxy for conservation focus. This suggests that management is applied to aid species were required.

While most conservation actions appear in place where required, certain conservation actions appear in need of improvement. This meta-analysis revealed a lack of correspondence between species suffering from native predators and native predator management. This limited correspondence may be explained by the controversy surrounding native predator management. The absence of correspondence and correlation between environmental stochasticity and translocations may be caused by the limitations of the assumption that this conservation action is directly aimed at this threat. Alternatively, more Procellariiform species in New Zealand are in need of translocations to mitigate the threats associated with stochastic events. The application of habitat management to species threatened by habitat loss also appears in need of improvement. This may indicate a limited focus within New Zealand on habitat loss as a threat to Procellariiformes, yet New Zealand has undergone a substantial reduction in native vegetation (Cieraad *et al.* 2015). On the other hand, a lack of literature discussing habitat loss as a threat to Procellariiform species in New Zealand might explain the distance in the MCA between species suffering from habitat loss and mitigating habitat management.

Publication bias may have been a factor while researching and compiling literature on the threats and conservation actions directed at New Zealand's Procellariiformes. This is a commonly encountered issue with meta-analyses (Rothstein *et al.* 2006, Fernandez-Duque & Vallegia 2010). The publication bias of this part of the study is likely to be smaller for conservation actions than for threats, as conservation actions in New Zealand appear well-documented, even if the results have not been published in peer-reviewed journals (e.g., through DOC reports). Some threats such as invasive species, net- and line fisheries seem thoroughly represented in the literature (e.g., Gaze 2000, Abraham & Thompson 2011, Abraham *et al.* 2013,

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Buxton *et al.* 2015). Other threats may be underrepresented in studies originating from New Zealand. For example, in Hawaii, considerable attention has been directed towards the impact of marine contaminants and plastic debris (Fry *et al.* 1987, Chu *et al.* 2015). In comparison, the literature on New Zealand based research addressing this threat appears only marginal (Buxton *et al.* 2013, Wilcox *et al.* 2015). A similar pattern may be present for light pollution affecting New Zealand's Procellariiform species, even though this threat is thoroughly documented from Macaronesia and the Mediterranean region (Rodrigues *et al.* 2012, Rodriguez *et al.* 2015). In addition, threats such as resource competition with humans and climate change are likely to be underrepresented in the literature, due to the potential difficulties of identifying these threats as direct or indirect causes of population declines.

Considering the range of threats and conservation actions of New Zealand's Procellariiformes, only few fall under the small population paradigm (Caughley 1994). Caughley (1994) proposed two defining paradigms to be present within conservation science: 1) the small population paradigm, and 2) the declining population paradigm. The first paradigm is concerned with the consequences of the smallness and rareness of a threatened population (e.g., inbreeding and stochasticity). The second paradigm is concerned with understanding the causes of the population declines and mitigating these (e.g., invasive species and habitat loss). Seabirds face a considerable suite of different threats that are included in the declining population paradigm and the majority of the assessed threat categories fall under this paradigm. The same pattern appears to hold for the conservation actions addressed in this metaanalysis. Environmental stochasticity affects most assessed species and this is the only assessed threat that falls under the small population paradigm. The only conservation actions that may be applicable to this paradigm is research directed at population dynamics and breeding biology research and translocations. The apparent lack of the small population paradigm in New Zealand's Procellariiformes may illustrate a limited appreciation in New Zealand for this paradigm. On the other hand, genetic threats to seabirds, such as inbreeding, appear surprisingly low, as these highly philopatric birds have been shown to actively choose to mate with close relatives (Cohen & Dearborn 2004) and breed in extreme proximity of their natal grounds (Steiner & Gaston 2005), perhaps to avoid outbreeding effects. Therefore, the

small population paradigm might not be as pressing to Procellariiform species as the declining population paradigm.

CONCLUSION

Based on the results from this qualitative meta-analysis, I show the variety of threats faced by New Zealand's Procellariiformes and the considerable number of conservation actions in place to address these threats. While certain gaps are present, the majority of conservation actions appear to be aimed directly at the relevant threats present. Conservation of New Zealand's Procellariiformes appears wellstructured overall, which is impressive, given the comparatively limited focus on and commitment to Procellariiformes conservation within New Zealand (Moller et al. 2000). Yet the assessment presented here should be seen as only the first step to improving conservation management. A quantitative assessment using seabird- or Procellariiformes-specific population models will provide much more detailed understanding of the impact of various threats faced by these species and the effectiveness of the mitigating actions. Due to the considerable lifespan and low fecundity (K-strategy) of Procellariiformes (Taylor 2000, Satterthwaite & Mangel 2012), a quantitative assessment will present considerable challenges, especially given the diversity of New Zealand's Procellariiformes (Moller et al. 2000, Croxall et al. 2012). While detailed data on population dynamics is present for a variety of threats and a limited suit of conservation actions (e.g., Fraser et al. 2011, Waugh et al. 2015), further long-term research is needed to improve understanding of future conservation challenges and directions. As Paleczny et al. (2015) showed that only 3% of seabird populations in New Zealand and surrounding waters have been monitored regularly, increasing monitoring efforts seems paramount to enable quantitative assessment of population dynamics and thus the magnitude of threats and success of conservation actions. Given the wide-ranging effects of Procellariiformes on their surrounding environment (Furness & Camphuysen 1997, Paleczny et al. 2015) and the importance of New Zealand for this order (Taylor 2000), continuing and improving current conservation management in New Zealand appears of global conservation interest.

Chapter 3

Chapter 3. NEST-SITE SELECTION OF SOUTH GEORGIAN DIVING PETRELS ON CODFISH ISLAND, NEW ZEALAND: IMPLICATIONS FOR CONSERVATION MANAGEMENT

ABSTRACT

MALL SEABIRD SPECIES are often threatened by predation from invasive species The their breeding colonies and considerable effort is invested into mitigating this threat. However, invasive predators may not be the only onshore threat affecting small seabird species. The South Georgian Diving Petrel (Pelecanoides georgicus; SGDP) is a small Procellariiform seabird species, considered Nationally Critical in New Zealand. My objective was to identify the terrestrial threats to the species at their sole remaining breeding colony in New Zealand on Codfish Island (Whenua Hou) following the successful eradication of invasive predators. To achieve my objective, I assessed the influence of five physical, three competition, and three plant variables on the nestsite selection of the SGDP with generalised linear models (GLMs) and compared models using an information theoretic approach. Models including the distance to the sea, slope, aspect and sand flux outperformed other models, and show selection for steep seaward-facing foredunes with mobile soils. In addition, no invasive plant- and competition variables were included in the best performing models, indicating that SGDPs neither avoid invasive vegetation, nor the vicinity of conspecifics, nor the vicinity of other seabird species. These results suggest that SGDPs are extremely vulnerable to effects caused by stochastic events and catastrophes, such as storms and storm surges. Eradication efforts directed at invasive predators on Codfish Island appear thus insufficient to safeguard the SGDP colony necessitating further conservation strategies to ensure the continued survival of this population.

INTRODUCTION

Seabird populations, considered good indicators of ecosystem health (Furness & Camphuysen 1997), have declined by 70% over the last 60 years (Paleczny *et al.* 2015). This is a concern, given that seabirds provide many important ecosystem services including nutrient cycling between pelagic and terrestrial ecosystems (Sekercioglu *et al.* 2004, Pelaczny *et al.* 2015, Chapter 2). Seabirds face threats on two fronts: at sea (e.g., accidental by-catch) and at their onshore breeding colonies (e.g., predation by invasive species) (Jones *et al.* 2007, Abraham & Thompson 2011). Smaller species are often more threatened onshore, while larger seabird species are more threatened at sea (Jones *et al.* 2007, Chapter 2).

New Zealand and its numerous offshore islands hosts one of the most diverse seabird communities and the highest number of endemic species globally (Taylor 2000). Local population trends mirror those found globally and as a consequence, New Zealand also has the most threatened seabird community in the world (Croxall *et al.* 2012) making their conservation of global importance.

New Zealand is considered a world leader in mitigating the negative effects of invasive predators on seabirds (Jones *et al.* 2016). Numerous eradication programmes have been implemented to control invasive species and protect seabird populations (Towns & Broom 2003). With increasingly better eradication techniques and protocols, larger islands have been successfully freed of their invasive predators (Towns & Broome 2003). Several seabird species have benefitted from these eradications (Ismar *et al.* 2014, Buxton *et al.* 2015), though the lack of sufficient posteradication monitoring of seabirds is concerning (Jones *et al.* 2016).

Despite the efforts aimed at the mitigation and eradication of invasive predators, other terrestrial factors, such as habitat loss, may also contribute to population declines or limit population recovery of seabirds (Taylor 2000, Chapter 2). However, these threats seem to receive less attention (Chapter 2). For example, studies directed at investigating exact habitat requirements of seabird species in New Zealand appear rare. Such studies should be encouraged, as habitat selection is one of the key components of ecological research and fundamental to understanding ecological processes (Johnson 1980, Manly *et al.* 2002). Understanding the mechanisms dictating how and why species choose specific habitats will enhance the

development of successful management strategies to preserve (seabird) species (Manly *et al.* 2002, Cassini 2013).

This conundrum is illustrated by the South Georgian Diving Petrel (*Pelecanoides georgicus*; SGDP) in New Zealand. The SGDP is a small burrow-breeding, Procellariiform seabird with a circumpolar distribution across the southern oceans. Due to its widespread distribution, the SGDP is globally considered Least Concern by the IUCN (2016). In New Zealand, however, the SGDP has declined steeply and was subsequently extirpated across most of its historic range (Worthy 1998, Taylor 2000, Holdaway *et al.* 2003, Wood & Briden 2008) (Figure 1). The only remaining SGDP colony in New Zealand currently persists in the dunes of the Sealers Bay on Codfish Island (Whenua Hou). The total SGDP population size on Codfish Island was estimated at 150 adults (Taylor 2013). Therefore, the species is currently considered Nationally Critical by the New Zealand Department of Conservation (DOC) (Robertson *et al.* 2013).

Underlying causes of decline of the SGDP in New Zealand remain speculative but predation by introduced species, such as Pacific rats (*Rattus exulans*), was likely a key contributor. However, while the removal of introduced predators (brush-tailed possums (Trichosurus vulpecula), Pacific rats, and Weka (Gallirallus australis)) from Codfish Island (Middleton 2007) initially resulted in an increased population trend of SGDPs between the 1980's and the late 1990's (Imber & Nilsson 1980, West & Imber 1989, Taylor 2000), this increase appears to have halted since 2000 (Taylor 2013). The reason for the lack of population growth is unknown, but several contributing factors have been hypothesised. For example, given that SGDPs in New Zealand nest in coastal dunes, the impact of encroachment of the dunes by (invasive) vegetation is currently perceived as a threat (Taylor 2013), even after the successful eradication of Marram Grass (Ammophila arenaria) and Mouse-eared Hawkweed (Pillosella officinarum) (Wickes & Rance 2010, Taylor 2013, DOC unpub. data). Due to the potential preference of SGDPs for coastal dunes for nesting, stochastic events and catastrophes such as storms might pose additional risks (Cole 2004). Furthermore, as Common Diving Petrels (P. urinatrix; CDP) recently have started breeding in the same dunes (Taylor & Cole 2002) competition for nest-sites might also pose a threat to the SGDP. No pelagic threats have yet been identified for the Codfish Island population (Taylor 2000), though collision with vessels caused by anthropogenic light pollution has been recorded for other populations (Black 2005).

To better understand potential onshore threats to the SGDP on Codfish Island, I conducted burrow searches and recorded a range of physical and biological variables at both burrows and random points between November 2015 and February 2016. I aimed to identify the most important dune characteristics influencing nest-site selection in SGDPs. Such information is essential to assess threats and identify conservation management options for the SGDP in New Zealand.

METHODS

Study area

I collected data on the nest-site selection of SGDPs in the Sealers Bay dunes (-46.766, 167.645) on Codfish Island (Whenua Hou), approx. 3 km west of Stewart Island (Figure 1). I defined the exact study area using an aerial photograph of Codfish Island (G. Elliott unpub. data 2004) geo-referenced to NZGD2000. The borders of the study area were defined by the Sealers Bay beach in the north, the forests of Codfish Island in the south and east, and an unnamed stream in the west. The size of this area was approx. 100 x 900 m, encompassing the entire Sealers Bay dunes and all SGDP burrows identified in previous surveys (Taylor & Cole 2002, Cole 2004).

Habitat selection

I assessed habitat selection within a use versus availability framework at the fourth scale of habitat selection (the selection of resources for one specific type of behaviour; Johnson 1980), i.e. nest-site selection. I considered SGDP burrows as used sites. To account for the available habitat, I created 150 random points within the entire study area using a random point generator in ArcGIS 10. At the study site, I marked random points with a bamboo/fibreglass pole and a track marker with an ID number. I discarded 19 random points, because they were located below the spring tide line.

As previous surveys (Imber & Nilsson 1980, Taylor & Cole 2002, Cole 2004) indicated a strong dependency on foredunes, I assessed habitat selection using two approaches: 1) habitat selection in the whole dune system, and 2) habitat selection in the foredune system. For the first approach, I included data from all random points (n

= 131) in the analyses. For the second approach I created a 20 m buffer around each detected burrow site in ArcGIS 10 and discarded all random points falling outside this buffer. The total number of remaining random points within these 20 m buffers was n = 45.

Burrow searches and occupancy assessment

I searched for burrows of Diving Petrels (*Pelecanoides* ssp.) and other Procellariiformes in the study area for ten days in November 2015. Burrow searches were made by walking the length of the dunes in pairs with 10 m distance between observers. I marked every detected burrow with a bamboo/fibreglass pole, a track marker with an ID number and a reflector (to enable safe navigation of the colony at night and minimize impact on breeding birds). In addition, I took a GPS point for each burrow.

I used various techniques to determine burrow occupancy. In November and December 2015, I monitored the burrows with stick palisades (Johnston *et al.* 2003) and checked these palisades twice per week. I considered burrows with more than three records of knocked over sticks as occupied to account for false positives (Taylor *et al.* 2012). To identify the species present in the burrows I used playback of calls of both SGDPs and CDPs in combination with hand capture of birds at night (Taylor & Cole 2002). In January 2016, I used burrow traps custom-made for *Pelecanoides* ssp. (length = 20 cm, \emptyset = 8 cm) at night to identify the occupants of remaining unidentified active burrows. Traps were checked every 45 to 60 minutes to prevent (heat) stress in these birds.

Variables affecting nest-site selection

I recorded a range of physical and biological variables at both burrows and random points. I identified plant species within a circle with 1 m² surface area, using Wilson (2009) and Wickes & Rance (2010) as references. I estimated the cover of each plant species as the vertical projection of all foliage onto a horizontal surface within this 1 m² circle. To reduce the number of explanatory variables, I summed the cover of all recorded plant species to form the variable plant cover. I also assessed the effect of invasive plant species such as Cock's Foot (*Dactylus glomerata*), Yorkshire Fog (*Holcus lanatus*), and Catsear (*Hypochaeris radicata*). To further reduce the number

of explanatory variables, I summed the cover of all invasive plant species which I then divided through the sum of the cover of all plant species to form the explanatory variable invasive plant ratio. Due to the high vegetation density at some sites, I refrained from measuring maximum standing vegetation height and instead classified plant height into one of five classes (0.0-0.5 m, 0.5-1.0 m, 1.0-1.5 m, 1.5-2.0 m, and > 2.0 m). I measured slope with a handheld clinometer. I measured aspect using a handheld compass and transformed recorded values to values between 2 and 0 using the Beers *et al.* (1966) transformation. The maximum aspect in this transformation was considered 45°, because the Sealers Bay dunes are a northeast facing dune system. I assessed soil compaction using a hand-held penetrometer (AMS Inc. G-281) with an adapter foot (AMS Inc. G-282) for sensitive soils (Ø 2.54 cm). With this penetrometer I measured the force needed to penetrate the soil to a depth of 6.4 mm in kg/cm². To account for micro scale variation I measured the soil compaction five times within a 1 m² circle at each site (at the centre and on the edge in each wind direction) and averaged values per site. I investigated sand flux by measuring the accumulation or erosion of sand at the poles marking the sites over the course of two months (49-66 days). I accounted for the difference in exposure time between sites by dividing sand flux (mm) through the number of days. I measured the distance to the sea, defined by the spring-tide line, the distance to the closest occupied SGDP burrow and the distance to other seabird species burrow in m in ArcGIS 10.

Data analysis

I constructed *a priori* models aligning with several biologically plausible hypotheses. I only included explanatory variables with Spearman correlation coefficients of $r \le 0.6$ in the same model. I then used generalised linear models (GLM) with a logit-link function to analyse nest-site selection of the SGDP. I applied the Akaike Information Criterion corrected for small sample sizes (AIC_C) (Burnham & Anderson 2002) to identify the relative importance of variables affecting nest-site selection by SGDPs. I also generated a "full" model (a model that includes all uncorrelated variables with the highest indicative fit) and a null model. For each model, I generated the AIC_C, the difference in AIC_C values relative to the best model (Δ AIC_C) and Akaike weights (w_i). I considered models with a Δ AIC_C < 4.0 to be supported by the data (Burnham &

Anderson 2002). I summed the w_i from all supported models to assess the relative importance of each variable (RVI).

The analysis of SGDP nest-site selection was then repeated, as explained above, for the 20 m buffer created around each burrow with the remaining dataset. However, I also accounted for biologically plausible interactions between explanatory variables in this second layer of analysis, as biotic variables in foredune habitats are under considerable pressure from abiotic influences (Hesp 1999).

All statistical analyses were conducted in Program R (R Development Core Team 2016) using the Hmisc (Harrel 2016) and MuMIn (Bartoń 2015) packages. I used the ggplot2 package (Wickham 2009) for visual interpretation, with Locally Estimated Scatterplot Smoothers (LOESS), of the most important variables affecting SGDP nest-site selection.

RESULTS

Burrow searches and occupancy

In total, 143 *Pelecanoides* ssp. burrows were found in the study area, of which 109 showed signs of occupancy. Using playback, hand captures and burrow traps 74 SGDP burrows, six CDP burrows and four burrows with mixed occupancy (one burrow was inhabited by a SGDP x CDP pair, two SGDP burrows were taken over by CDPs and one CDP burrow was taken over by SGDPs) were identified. The occupants of 25 *Pelecanoides* ssp. burrows remained unidentified. In addition, seven larger burrows were found inhabited by Sooty Shearwaters (*Puffinus griseus*).

Relative importance of variables in the whole dune system

Distance to sea was highly correlated ($r \ge 0.6$) with distance to nearest conspecific, plant cover and plant height (Appendix 4). Distance to nearest conspecific was also highly correlated with plant cover and plant height. In addition, plant cover was highly correlated with plant height. Therefore, these dune variables were not included in the same models.

Distance to sea, slope, aspect, sand flux and penetration were all explanatory variables present in the best performing models (AICc < 4.0; Table 7). Distance to sea, slope and aspect were the most important variables for SGDP nest-site selection (RVI = 0.961; Table 8), followed by sand flux (RVI = 0.861) and sand penetration (RVI = 0.381). The relationship between SGDP nest-site selection and the distance to the sea was negative (Table 8 and Figure 6). The relationship between SGDP nest-site selection and slope, aspect and sand flux was positive, while the relationship with sand penetrability was negative. SGDP thus selected for dunes within 20 m distance from the sea (foredunes) with steep, northeast (seaward) facing slopes, high sand flux and, loose soils. Competition and plant parameters were not included in the best models.

the difference in AIC _c relative to the model most supported by the data (Δ AIC _c) and Aka	ike weight	ts (<i>w</i> i) for ne	st-site select	ion by
South Georgian Diving Petrels in the whole dunes. Models with a $\Delta AIC_C < 4$.0 (bold) are	considere	d to be supp	orted by the	data.
Candidate models	Я	AICc	ΔΑΙCc	Wi
Distance to sea + slope + aspect + sand flux	4	123.2	0	0.479
Distance to sea + slope + aspect + sand flux + sand penetrability	ß	123.6	0.4	0.382
Distance to sea + slope + aspect	3	126.3	3.1	0.100
"Full" model	8	128.4	5.2	0.035
Distance to nearest conspecific + slope + aspect + sand flux	4	134.6	11.4	0.002
Distance to nearest conspecific + slope + aspect + sand flux + sand penetrability	IJ	134.6	11.4	0.002
Distance to nearest conspecific + slope + aspect	33	134.8	11.6	0.001
Invasive ratio + slope + aspect + sand flux + sand penetrability	IJ	153.2	30.0	0.000
Distance to sea	1	153.7	30.5	0.000
Slope + aspect + sand flux + sand penetrability	4	155.9	32.7	0.000
Plant cover + slope + aspect + sand flux + sand penetrability	ы	157.9	34.7	0.000
Plant cover + slope + aspect + sand flux	4	163.0	39.8	0.000
Plant cover + slope + aspect	ŝ	168.3	45.1	0.000
Distance to nearest conspecific	1	178.5	55.3	0.000
Plant height	-1	237.4	114.2	0.000
Plant cover	1	253.8	130.6	0.000
Distance to nearest <i>Pelecanoides urinatrix</i>	7	270.1	146.9	0.000
Invasive ratio	1	270.1	146.9	0.000
Null model	0	270.2	147.0	0.000
Distance to nearest Puffinus griseus	1	270.8	147.6	0.000

model), number of explanatory variables included in models (K), Akaike Information Criteria corrected for small sample sizes (AICc), Table 5. Candidate models (including a "full" model that includes all uncorrelated variables with the indicative highest fit and a null



(as defined by the spring tide line) in m. 6B: Slope in °. 6C: Aspect, transformed following Beers et al. (1966), with northeast (seaward) important explanatory variables affecting nest-site selection of South Georgian Diving Petrels in the whole dunes. 6A: distance to sea Figure 6. Scatterplots and Locally Estimated Scatterplot Smoothers (LOESS) including 95% confidence intervals for the four most facing slopes receiving a value of 2 and southwest (land inward) facing slopes receiving a value of 0. 6D: sand flux in mm/day. **Table 6.** Regression coefficients (β), standard errors (SE) and relative variable importance (RVI) for explanatory variables included in the best preforming nest-site selection models for South Georgian Diving Petrels in the whole dunes (AICc < 4.0). * indicates that $\beta \pm 2$ * SE does not intersect 0.

Variable	β	SE	RVI
Distance to sea	-0.188*	0.033	0.961
Slope	0.105*	0.016	0.961
Aspect	2.090*	0.411	0.961
Sand Flux	0.759*	0.315	0.861
Sand penetrability	-23.950*	3.987	0.381

Relative importance of variables in the foredune

No explanatory variables were highly correlated in the foredune (Appendix 5). In the foredune, distance to sea, slope, aspect, sand flux and plant cover were explanatory variables present in best performing models (Table 9). Distance to sea, slope, aspect, and plant cover were important factors for SGDP nest-site selection (RVI = 0.843). Sand flux appeared less important in the foredune (RVI = 0.317). There was a positive relationship between SGDP nest-site selection and slope and aspect, while there was a negative relationship with the distance to the sea (Table 10). Within the foredune, SGDPs thus also selected for dunes close to the sea with steep seaward-facing slopes. Furthermore, the interactions between the distance to sea and physical dune variables proved influential as well as the interactions between plant cover and the physical dune variables (Table 10 and Figure 7). Within the foredune no competition variables were included in the best performing models and neither were invasive plant ratio and plant height.

Table 7. Candidate models (including a full and a null model), number of explanatory	variables includ	ed in models (K), Akaike	
Information Criteria corrected for small sample sizes (AICc), the difference in AICc rel	tive to the mode	l most supported by the c	data
(ΔAIC_c), and Akaike weights (w_i) for nest-site selection by South Georgian Diving Petr	els in the foredu	ie. Models with a ΔAIC_C <	< 4 .0
(bold) are considered to be supported by the data.			
Candidate models	K AIC	c ΔΑΙCc ν	Wi

Candidate models	K	AICc	ΔAIC_{C}	Wi
(Slope + aspect) * (plant cover + distance to sea)	8	104.0	0.0	0.526
(Slope + aspect + sand flux) * (plant cover + distance to sea)	11	105.0	1.0	0.317
(Slope + aspect + sand flux + sand penetrability) * (plant cover + distance to sea)	14	108.6	4.7	0.051
(Slope +aspect) * plant cover	ъ	108.7	4.7	0.049
(Slope + aspect + sand flux) * plant cover	7	111.7	7.7	0.011
(Slope + aspect + sand flux) * distance to sea	7	111.8	7.8	0.011
(Slope + aspect + sand flux + sand penetrability) * plant cover	6	111.9	7.9	0.010
(Slope + aspect + sand flux + sand penetrability) * distance to sea	6	112.0	8.1	0.009
(Slope + aspect) * distance to sea	S	112.7	8.7	0.007
Full model	11	114.2	10.3	0.003
Slope + aspect + sand flux + distance to sea	4	114.7	10.8	0.002
Slope + aspect + sand flux	ŝ	115.1	11.2	0.002
Slope + aspect + sand flux + sand penetrability	4	115.9	11.9	0.001
(Slope + aspect + sand flux) * (invasive ratio + distance to sea)	11	117.8	13.8	0.001
(Slope + aspect + sand flux + sand penetrability) * (invasive ratio + distance to sea)	14	121.4	17.4	0.000
(Slope + aspect + sand flux + sand penetrability) * (invasive ratio)	6	121.5	17.5	0.000
Invasive ratio * distance to sea	æ	133.4	29.5	0.000
Plant cover * distance to sea	æ	134.6	30.7	0.000
Distance to sea	1	139.2	35.2	0.000
Plant height	1	155.7	51.7	0.000
Distance to nearest conspecific	1	157.5	53.5	0.000
Plant cover	1	158.8	54.9	0.000
Distance to nearest Puffinus griseus	1	159.0	55.0	0.000
Invasive ratio	1	159.8	55.9	0.000
Null model	0	159.9	55.9	0.000
Distance to nearest <i>Pelecanoides urinatrix</i>	1	160.9	56.9	0.000

Table 8. Regression coefficients (β), standard errors (SE) and relative variable importance (RVI) for explanatory variables included in the best preforming nest-site selection models for South Georgian Diving Petrels in the foredune (AIC_c < 4.0). * indicates that $\beta \pm 2$ * SE does not intersect 0.

Variable	β	SE	RVI
Slope	0.090*	0.019	0.843
Aspect	2.052*	0.531	0.843
Plant cover	0.976	0.672	0.843
Plant cover : slope	0.053	0.070	0.843
Plant cover : aspect	4.061*	1.928	0.843
Distance to sea	-0.162*	0.039	0.843
Distance to sea : slope	0.006	0.004	0.843
Distance to sea : aspect	0.205	0.133	0.843
Sand Flux	-0.114	0.320	0.317
Plant cover : sand flux	0.558	1.120	0.317
Distance to sea : sand flux	0.071	0.067	0.317



Figure 7. Explanatory variables and interactions affecting nest-site selection in South Georgian Diving Petrels in the foredunes. "Physical" consists of a cluster of slope, aspect and sand flux.

DISCUSSION

My results show that SGDP nest-site selection is dictated by the distance to the sea, physical dune variables (slope, aspect, sand flux and, to some extent, sand penetrability) and plant cover. SGDPs select for foredunes with steep seaward facing slopes and mobile soils. Interactions between physical variables and the distance to the sea as well as interactions between physical variables and plant cover also affect nest-site selection in SGDPs. Competition or invasive plants do not affect SGDP nest-site selection.

The strong preference of SGDPs to nest in dunes close to the sea (not further than 20 m inland) is best explained by need for these birds to have a close "runway" for easy departure from the island. SGDPs have relatively short, paddle-like wings adapted to wing-propelled diving (Onley & Scofield 2007) and may therefore struggle to take off under certain circumstances. On calm nights, I observed that birds ran down onto the Sealers Bay beach and use it as a "runway" in order to take off. Steep seaward-facing dunes provide easy take-off sites and direct access to the sea during windy nights.

The preference for sites with mobile and loose soils might be caused by an inclination of SGDPs to construct nests in soils that allow easy burrowing and are freedraining. The SGDPs breed in relatively deep burrows (up to 2 m), which are excavated by the birds. It should be noted that my assessment of penetrability was limited to the uppermost sand layer. Further assessment of the penetrability of deeper soil layers is likely to provide further insights on the effect of sand penetrability on SGDP nest-site selection.

Biotic and abiotic variables affect each other in dynamic ecosystems such as foredunes. For example, the distance to the sea shapes the physical variables in the foredunes (Hesp 1999). The exact interactions between physical variables and overlaying plants remain poorly understood, as physical dune characteristics will influence plants (e.g., Sykes & Wilson 1990, French 2012, Murphy *et al.* 2012), but plants can also shape dune profiles by changing physical variables (Hesp 1999). Therefore, it is not surprising that SGDP nest-site selection is affected by interactions between multiple variables. Further investigations will be necessary to unravel how different variables affect each other and consequently the SGDP nest-site selection.

Given the preference of SGDPs for steep seaward-facing and mobile foredunes, this species is very susceptible to stochastic events and catastrophes such as storms during the breeding season. Storms are already impacting SGDPs on Codfish Island. In 2003 a storm extirpated at least 15% of the population, destroyed 40% of the nests and removed the first 10 m of the dunes (estimated at 23,377 m³ of sand; Cole 2004). Unfortunately, storm events and storm surges are likely to increase in both intensity and severity in New Zealand due to human-induced climate change (Blair 2007, Hennessy *et al.* 2007). If a similar event were to be repeated, 67 burrows (91%) might be lost, as they were located within the first 10 m of dunes above the spring tide line.

Even under the assumption that, if only the burrow entrance is affected and the burrow might still be successful, 49 burrows (66%) are still at direct risk of another storm event (as burrows are roughly 2 m long). Therefore, severe storms and storm surges during the breeding season are likely to be the most detrimental current threat to SGDPs on Codfish Island.

Avoidance of conspecifics and other Procellariiformes species does not appear to prominently factor into nest-site selection of SGDPs. However, as three SGDP nests failed due to interactions with CDPs (including the mixed pair), CDPs do appear to compete with SGDPs for some nest-sites (Chapter 4). Competition for nest-sites with other, more abundant Procellariiformes, is common in New Zealand. For example, the Chatham Petrel (*Pterodroma axillaris*) was put at extreme risk of extinction by nestsite competition with the aggressive Broad-billed Prion (*Pachyptila vittata*) (Gardner & Wilson 1999, Sullivan & Wilson 2001, Gummer *et al.* 2015), which vastly outnumbered Chatham Petrels. In the case of possible nest-site competition between the SGDP and the CDP, the threatened species still outnumbers the competing species within the colony. However, CDPs appear to be more aggressive than SGDPs (S. Trainor pers. comm. 2016) and if the number of CDPs within this colony increases, they may well form a significant threat to the SGDPs in the future.

My results showed that SGDP nest-site selection is not influenced by invasive plant species. This may have been due to the recent successful eradication of Marram Grass and Mouse-eared Hawkweed from the Sealers Bay dunes (Wickes & Rance 2010, Taylor 2013, DOC unpub. data). Localised removal of Marram Grass on the Chatham Islands, New Zealand, has allowed the Endangered Chatham Island Oystercatcher (*Haematopus chathamensis*) to breed further away from the high tide line (Moore & Davis 2004, IUCN 2016). This action reduced the impact of storms and storm surges for this species. However, there is no evidence that supports a movement of SGDP burrows further inland since the eradication of Marram Grass on Codfish Island. The only common invasive plant species within the SGDP colony are currently Cock's Foot, Yorkshire Fog, Catsear, and Hawkbit (*Leontodon taraxacoides*). These species might not be strong sand binders and therefore do not influence physical variables in the dunes. However, the Sealers Bay dunes remain vulnerable to (re)invasion of notorious sand binders, as the (re)discovery of several individuals of the invasive Purple Groundsel (*Senecio elegans*) within the dunes illustrated. Thus

continued biosecurity and vegetation monitoring of the dunes should be part of future monitoring efforts.

The results showing SGDP preference for fragile foredunes provide an initial step towards understanding the exact mechanisms of nest-site selection in the SGDP. For example, many Procellariiformes show strong nest-site fidelity (Miskelly *et al.* 2009). Foredunes are inherently mobile and dynamic (Hesp 1999), therefore it is possible that dune variables dictating nest-site selection may change over time. Given the short-term nature of my study, a continued multi-year monitoring programme of the SGDP population in combination with a study assessing nest-site selection of new burrows is recommended.

CONCLUSION

Eradication of invasive predators may sometimes be insufficient to aid population recovery of small seabirds. The past eradication efforts on Codfish Island were aiming to facilitate population recovery of several small seabird species (Middleton 2007). However, other terrestrial threats can also be present and may be preventing recovery, as illustrated here by the vulnerability of South Georgian Diving Petrels to stochastic events, caused by their dependency on fragile foredunes. Consequently, continued monitoring after eradication efforts is necessary to identify such threats, and additional conservation measures may be required to ensure population recovery of certain species, including the South Georgian Diving Petrel on Codfish Island. Chapter 4

Chapter 4. ASSESSING THE SUITABILITY OF NON-INVASIVE METHODS TO MONITOR INTERSPECIFIC INTERACTIONS AND BREEDING BIOLOGY OF THE SOUTH GEORGIAN DIVING PETREL

ABSTRACT

REDATION BY INVASIVE mammals has devastated New Zealand's seabird populations. However, seabirds also face a variety of other threats including competition for nest-sites (burrows). Furthermore, the habit of breeding in burrows, limits breeding biology studies in many small seabirds. I assessed the potential impact of interspecific interactions on the breeding success of the South Georgian Diving Petrel (Pelecanoides georgicus), a Nationally Critical seabird species in New Zealand, by monitoring 20 burrows with remote cameras and stick palisades. Additionally, I tested the use of remote cameras to non-invasively study the breeding biology and activity patterns of the South Georgian Diving Petrel by pairing five remote cameras with Radio Frequency Identification (RFID) readers. I recorded seven species at SGDP burrows. One species caused two monitored burrows to fail: the Common Diving Petrel (*P. urinatrix*), which thus may pose a potential threat to the South Georgian Diving Petrel. These results suggest that remote cameras are useful tools to study interspecific interactions at seabird burrows. However, cameras had extremely low detection rates ($\bar{x} = 10.86\% \pm 7.62\%$) when compared to RFID readers. The low detection rates of South Georgian Diving Petrel activity at their burrows may be explained by their small body size and the speed at which birds enter and exit burrows. Therefore, remote cameras, or at least the model we used, appear unsuitable to study breeding biology and activity patterns in this, and possibly other small burrowing seabirds.

INTRODUCTION

Seabirds are one of the most threatened taxonomic groups on the planet (Croxall *et al.* 2012). Due to their life history, seabirds are threatened on two fronts: on land and at sea (Taylor 2000). Invasive mammalian predators, such as rats (*Rattus* ssp.), are considered one of the most detrimental terrestrial threat to seabirds in general, and smaller species in particular (Jones *et al.* 2007, Chapter 2). However, substantial effort is being invested into mitigating their impacts through island-wide eradications (Towns & Broome, Jones *et al.* 2016). In New Zealand, home to one of the most diverse and threatened seabird communities on the planet, invasive mammalian predators have severely decimated the abundance and distribution of seabird species and populations (Taylor 2000, Croxall *et al.* 2012).

Besides invasive mammals, the already decimated seabird populations in New Zealand face several other threats on shore, including habitat loss and effects of stochastic events (Taylor 2000, Chapter 2 & 3). Furthermore, interspecific interactions, other than predation by invasive species, can impact seabird populations (Friesen *et al.* 2016, Chapter 2). Various cases of negative interactions with native species have been documented, including Morepork (*Ninox novaeseelandiae*) predation, non-predatory attacks by Campbell Island Teals (*Anas nesiotis*), and competition between various seabird species for nest-sites (Sullivan & Wilson 2001, Trainor 2008, Friesen *et al.* 2016, Sagar *et al.* 2016). In some instances, such interactions have contributed to extreme population declines (Sullivan & Wilson 2001).

Many small seabird species in New Zealand breed in burrows, restricting our ability to study breeding biology and activity patterns. To overcome this limitation, several techniques have been used. The simplest method to monitor activity patterns is the use of stick palisades (a row of sticks in front of the burrow entrance), but this method is prone to false positives (Taylor *et al.* 2012). An approach to study both activity patterns and breeding biology is the instalment of study burrows (the placement of a door into a burrow that allows the access to brood chambers). However, the use of study burrows is labour intensive, invasive and may not always be feasible (Blackmer *et al.* 2004, Taylor *et al.* 2012). In more recent years, the development of new technologies has produced less invasive study methods. For

example, Radio Frequency Identification (RFID) readers, also known as Passive Integrated Transponder (PIT) readers, have been used to study small burrowing seabirds (e.g., Zangmeister *et al.* 2009, Taylor *et al.* 2012). RFID readers allow the automated monitoring at burrow entrances of individuals equipped with RFID tags. Additionally, remote cameras are increasingly being used to monitor burrows and assess breeding biology and activity patterns (Taylor *et al.* 2012, Dilley *et al.* 2015). However, the use of remote cameras poses considerable challenges, as large amounts of footage need to be viewed and assessed (Johnston *et al.* 2003). On the other hand, remote cameras provide the opportunity to assess interspecific interactions at burrows (Dilley *et al.* 2015).

The South Georgian Diving Petrel (*Pelecanoides georgicus*; SGDP) is a small, burrowing seabird species. The SGDP is considered Nationally Critical in New Zealand (Robertson *et al.* 2013), because it is limited to Codfish Island (Whenua Hou) (Figure 1) and the population numbers a mere 150 individuals approximately (Taylor 2000). Codfish Island is free of invasive predators following eradication efforts (Middleton 2007). Invasive species are likely to have been the main cause of the historic population declines in this species (Taylor 2000). However, dune erosion, caused by storms, continues to threaten this small SGDP colony (Chapter 3). Furthermore, interactions with other species may also reduce the reproductive success of this species. For example, the SGDP may suffer from competition for nest-sites with the Common Diving Petrel (*P. urinatrix*; CDP) (Chapter 3). In addition, Morepork predation has been recorded anecdotally (Trainor 2008). Currently available data on the SGDP breeding biology and activity patterns are either anecdotal (Taylor & Cole 2002, Cole 2004, Trainor 2008, Trainor 2009) or originate from populations from different oceans (Payne & Prince 1979, Marchant & Higgins 1990).

To gain a better understanding of interspecific interactions affecting SGDP breeding success on Codfish Island, I monitored 20 occupied SGDP burrows with remote cameras during the presumed chick rearing period (Taylor 2013). In addition, to assess the utility of remote cameras to monitor and study the breeding biology and activity patterns of the SGDP, I paired five remote cameras with RFID readers.

METHODS

Study area

The SGDP in New Zealand is limited to one colony at the Sealers bay dunes (-46.766, 167.645) on Codfish Island, approx. 3 km west of Stewart Island (Figure 1). I defined the exact study area using aerial photographs (G. Elliott unpub. data 2004) georeferenced to NZGD2000 and maps of previous SGDP nest-sites (Taylor & Cole 2002). The exact study area encompassed the entire Sealers bay dunes and was limited by natural borders: the Sealers beach in the north, forest in the south and the east, and a creek in the west. The size of the study area was approx. 100 x 900 m.

Assessment of burrow occupancy and breeding success

I searched for burrows during the first 10 days of field work (early November 2015) by walking the length of the study area. I assessed the occupancy of identified burrows using stick palisades, which were checked twice a week. To account for false positives (Taylor *et al.* 2012), I only considered burrows with three or more records of disturbed palisades as active. I then used hand captures and playback to confirm that SGDPs were the species occupying the burrows (Taylor & Cole 2002). To assess burrow abandonment, I continued to check stick palisades twice a week until late December 2015.

During a repeat visit in late January 2016, I assessed the success (i.e. producing fledgings) of all SGDP burrows using daily monitoring with stick palisades (Taylor & Cole 2002). I assumed burrows to have chicks close to fledging when repeated signs of activity (disturbed palisades) were recorded. I assumed that burrows successfully produced fledglings, if active burrows seized to show signs of activity in late January 2016.

Remote camera pilot study

I assessed the most suitable settings in Bushnell Trophy Cam[™] Trail Cameras (Model 119436; Bushnell Outdoor Technology 2011) for long-term monitoring of SGDP burrows using 10 cameras in early November 2015. This initial round of testing showed that these cameras recorded almost indefinitely throughout the day, potentially due to the high temperature differences in dunes affecting the Passive

Infrared (PIR) sensor of the camera (Bushnell Outdoor Technology 2011). This caused memory cards to fill up within days. In addition, SGDPs appeared to enter/leave their burrows in seconds, without lingering at burrow entrances. Therefore, I decided to use the following settings for long-term monitoring at SGDP burrows: 5 second video recordings, 60 second break period and "medium" sensitivity (Bushnell Outdoor Technology 2011).

Assessment of interactions at burrows

I deployed 20 cameras to assess the interactions of various species with SGDP burrows. I randomly selected 15 occupied SGDP burrows. Five additional cameras were placed at burrows that were occupied by birds fitted with RFID tags (see below). This selection of monitored burrows spanned the whole length of the study area. I monitored all 20 burrows from mid-November 2015 to late January 2016 (54-61 monitoring nights) and consequently, covered the entire presumed chick rearing period (Taylor 2013) with a cumulative total of 1121 monitoring nights. I replaced all memory cards and downloaded data on a weekly basis. I replaced broken or malfunctioning cameras when necessary.

Assessment of remote cameras for monitoring

I captured SGDPs by hand at burrow entrances to equip birds with RFID tags to assess SGDP detection rates of remote cameras. When the burrow surroundings were feasible for RFID reader placement (e.g., flat ground with relatively stable soils), I attached a small (12 x 2.5 mm) RFID tag (Allflextm P/N, ISO FDX-B). I placed RFID tags externally on the left tarsus using wrap-around colour bands, as previous attempts at internal RFID placement resulted in excessive bleeding in SGDPs (Trainor 2009). Due to low success rates of hand capture, only five birds from different burrows were fitted with an RFID tag. Considerable amount of time was invested in capturing the partner of these five birds, but without success. RFID tagged birds were marked with a lateral stripe on the crown using Wite-Out[®] to allow individual recognition on remote cameras. None of the tagged birds showed any change in behaviour.

After birds were equipped with RFID tags, I deployed five remote cameras and five RFID readers in a paired setup at their burrows. I used small, light-weight, waterproof, custom-made RFID readers as used in Taylor *et al.* (2012). The internal

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settings of these readers allow for adjustment of the recording time and I set them to record from 2100 h to 0600 h. In addition, I programmed the RFID readers to read for potential tags every 0.1 second to ensure maximum detectability. I built customised RFID reader antennas using transformer-winding, copper wire on site following Taylor *et al.* (2012), to ensure appropriate correspondence with the RFID tags (134200 Hz). The reading frequency of the antennas was checked weekly to ensure it remained constant (Taylor *et al.* 2012). The RFID readers ran on 12 V batteries, which were replaced on a weekly basis. I monitored SGDP burrows with RFID readers for 28-34 nights from mid-November to late December 2015.

Data analysis

To assess interspecific interactions at SGDP burrows, I checked all videos recorded between sunset and sunrise, as SGDPs arrive at their burrows after sunset and return to sea before sunrise (Taylor & Cole 2002). I recorded activities of all species detected at SGDP burrow entrances and categorised activities based on the interaction with SGDP burrows: neutral (i.e. no perceivable interaction with the SGDP burrow), investigative (e.g., inspecting the burrow entrance) and interfering (i.e. competition or predation). I considered multiple videos of a certain species (other than SGDP) in a single night as one record. To assess the effect of these interactions on SGDP breeding success, I linked the recorded interaction to stick palisades records.

To assess the use of remote cameras for SGDP breeding biology monitoring, I compared the time RFID readers recorded SGDP activity with the time of remote camera records. SGDP records with 5 minutes of overlap between remote cameras and RFID readers were considered to pertain to the same record, as both RFID readers and remote cameras can have some error in recording time. Multiple RFID detections within 1 minute were reduced to one record, to account for the 60 second break period of the remote cameras. I considered RFID reader detections as 100% reliable (Taylor *et al.* 2012) and calculated remote cameras, but not by RFID readers were assumed to pertain to the untagged partner, if the Wite-Out® marking was not visible. In addition, as birds may leave burrows too quickly to be recorded on the remote cameras, while still triggering the camera (the used type of remote cameras has a response period of 1 second; Bushnell Outdoor Technology 2011), I considered videos

without SGDPs that were recorded at the same time as RFID detected SGDP activity as "near-hits". I combined percentages of SGDP detections and "near-hits" to assess the total detection rates of the cameras. Furthermore, I categorised SGDP activity on videos as entering or exiting.

I refrained from statistical analyses as sample sizes were small, but conducted percentage calculations and graphical visualisations using Program R (R Development Core Team 2016) with the ggplot2 package (Wickham 2009).

RESULTS

Interactions at burrows

I obtained 20,897 videos at 20 SGDP burrows during the presumed chick rearing period. Of those videos, 1616 were recorded at night and these revealed 88 videos of seven different species. The most commonly recorded species were Little Blue Penguin (*Eudyptula minor*) (recorded at 9 burrows; 14 records), Kakapo (*Strigops habroptilus*) (7 burrows; 9 records), and Blackbird (*Turdus merula*) (5 burrows; 6 records). CDPs were recorded at two burrows (14 records), while Yellow-eyed Penguins (*Megadyptes antipodes*), Sooty Shearwaters (*Puffinus griseus*) and Campbell Island Teals were rare and only recorded at one single burrow. The majority of interspecific interactions recorded at SGDP burrows were neutral (Figure 8). However, Kakapo occasionally showed investigative behaviour (Figure 9A). More importantly, all records of CDPs showing signs indicative of physical conflict, and CDPs collecting nesting material (Figure 9B).

Ten of the 20 monitored SGDP burrows did not successfully produce fledglings. For two of the unsuccessful burrows this was directly linked to the interference of another species, the CDP, as no SGDP activity was recorded after the recorded interfering behaviour. For the other eight unsuccessful SGDP burrows, the cause of abandonment remained unidentified.

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Figure 8. Nature and frequency (mean ± standard error of mean) of nocturnal interspecific interactions at South Georgian Diving Petrel burrows, as recorded with remote cameras.



Figure 9. Investigative and interfering behaviour of two species at South Georgian Diving Petrel burrows recorded by remote cameras. 8A shows a Kakapo investigating a burrow entrance. 8B shows a Common Diving Petrel in the burrow entrance, collecting nesting material, and showing with signs of previous physical conflict (as indicated by the disorderly feathers on the side of the head).

Detection rate of remote cameras

During the study period, RFID readers detected 33-38 SGDP records at successful burrows (n = 3), while RFID readers at unsuccessful burrows (n = 2) detected only 8-12 SGDP records. The nocturnal SGDP activity recorded by RFID readers showed two activity peaks: around 2300 h and around 0300 h (Figure 10). Remote cameras detected 3-13 SGDP records at successful burrows and none at unsuccessful burrows. Of the activities detected by remote cameras only two pertained to birds leaving their burrow, while all others (n = 15) related to birds entering. Furthermore, the activity patterns revealed by remote cameras differed substantially from the patterns revealed by RFID readers.

When compared to RFID readers, the detection rates of remote cameras were extremely low. Detection rates ranged from 0.00% to 40.63% ($\bar{x} = 10.86\% \pm 7.62\%$). "Near-hit" rates were slightly higher and ranged from 0.00% to 47.49% ($\bar{x} = 24.94\% \pm 8.99\%$) of RFID reader detections. When combined, the total detection rates ranged from 0.00% to 62.50% ($\bar{x} = 35.81\% \pm 16.60\%$). No remote camera records of marked birds remained undetected by the RFID readers, indicating accurate detection rates of RFID readers.



Figure 10. Nocturnal activity of South Georgian Diving Petrels recorded by two noninvasive monitoring methods.

DISCUSSION

My results show that several species do occur at, and interact with SGDP burrows, but only two species showed intentional interactions (investigative/interfering), of which only the CDP impacted the breeding success of the SGDPs. These results suggest that remote cameras may be a useful tool to assess the impact of adverse interactions at SGDP burrows. However, my results also show that remote camera detection rates of SGDP activity are extremely low and resulted in questionable activity patterns. Therefore, this non-invasive monitoring method appears unsuitable to study breeding biology and activity patterns in the SGDP.

Monitored SGDP burrows were negatively affected by CDP behaviour. No SGDP activity was recorded at these burrows after the initial records of CDPs, and CDPs were collecting nesting material at these burrows. Data thus suggest that these SGDP burrows were taken over by CDPs. It remains unknown whether or not the recorded interfering behaviour resulted in the mortality of any SGDPs, but it is conceivable that the interaction with CDPs resulted in the failure of these two burrows. Currently, the CDP population is very small (Chapter 3) and thus the threat from CDP competition may be only minor. Continued monitoring is needed to assess the CDP population trends within the Sealers bay dunes, and to quantify the potential negative effect on the SGDP. Previous observations suggested that the CDP may be more aggressive than the SGDP (S. Trainor pers. comm. 2016). If the CDP population or records of SGDP-CDP competition increase substantially, competition management may be required to safeguard the SGDP population.

Several other species were recorded at SGDP burrows; however, none showed any behaviour with negative effects on SGDP breeding success. Kakapo activity at SGDP burrows was detected comparatively often and the species even investigated burrows, but Kakapo do not appear to pose a threat to SGDP breeding success. The Kakapo is a strictly herbivorous species that has an intricate breeding system with nest-sites in forested habitat (Lloyd & Powlesland 1993). Therefore, the interest of this species in some SGDP burrows is more likely due to the inquisitive nature of this species (Farrimond *et al.* 2006). The presence of cameras even may have attracted curious Kakapo to SGDP burrows and therefore elevated the amount of records on remote cameras. In addition, a single record of Campbell Island teal, showing neutral

behaviour, was made throughout the presumed SGDP chick rearing period. This species is capable of reducing the breeding success of Mottled Petrel (Pterodroma inexpectata) through non-predatory attacks (Sagar et al. 2016). However, the lack of interactions recorded, indicates that teals are not impacting the SGDPs, perhaps because their breeding periods coincide (Heather & Robertson 2015). Campbell Island Teals may be more reclusive during the breeding period (R. Sagar pers. comm. 2016), potentially reducing encounter rates between teals and SGDPs. Mottled Petrels have a more prolonged breeding season that overlaps less with the Campbell Island Teal breeding season (Heather & Robertson 2015) and hence encounter rates between these two species may be higher. Alternatively, the small size of SGDP burrows may prevent non-predatory attacks from Campbell Island Teals. Furthermore, remote cameras did not record Moreporks throughout the presumed SGDP chick rearing period. Moreporks predate on small birds (Haw & Clout 1999), including SGDPs (Trainor 2008). The chick rearing period is likely to be the time when SGDPs are most vulnerable to Morepork predation, as adults enter and exit their burrows virtually every night to feed their chicks (Payne & Prince 1979, Marchant & Higgins 1990, Taylor & Cole 2002). Therefore, the record of SGDP predation by a Morepork (Trainor 2008) may have been incidental and thus Moreporks may not pose a considerable threat to the SGDP population.

Although, remote cameras have low detection rates of SGDP activity, it is probable that interactions between species get recorded because interactions are likely more prolonged than birds entering/exiting burrows. For eight of the unsuccessful monitored burrows the cause remains unknown and this could pertain to interspecific interactions missed by the remote cameras. However, seabird colonies often consist of a mix of breeding birds, unpaired birds, and pre-breeding age prospecting birds, and distinguishing these groups can be difficult (Warham 1996). Therefore, it is more likely that these unsuccessful burrows related to unpaired or prospecting birds, instead of burrows that failed due to undetected interactions. Remote cameras therefore appear a useful tool to assess the effect of interspecific interactions on the breeding of the SGDP, and potentially other small burrowing seabirds.

As useful as remote cameras are to monitor interspecific interactions, the detection of SGDP activity was very low and resulted in inaccurate activity patterns.

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Remote cameras of the used model were thus not suitable to monitor the breeding activities of the SGDP. Potentially, the detection rates were low, because SGDPs enter and leave their burrows quickly, probably to avoid predation (Watanuki 1986, Mougeot & Bretagnolle 2000). The higher detection rate of SGDPs entering burrows may be explained by the need to clear the burrow entrances of accumulated sand. It should be noted that remote cameras are constantly improving (Swann et al. 2011). Newer models may be less prone to record indefinitely in dune habitats, allowing higher sensitivity settings and may thus be more suitable for the monitoring of SGDPs. Furthermore, remote cameras with Active Infrared (AIR) sensors are also less prone to false triggers, but are substantially more expensive (Kays & Slauson 2008). The model we used may be more advantageous in other (seabird) species, for most other small burrowing seabird species do not breed in dunes. However, other small burrowing seabird species are likely to enter and leave their burrows equally quickly to avoid predation (Watanuki 1986, Mougeot & Bretagnolle 2000), which may result in equally low detection rates. Therefore, the use of remote cameras to study breeding biology and activity patterns in small, burrowing seabirds should be considered with care, as this method may not be the most advantageous.

The use of RFID readers for breeding biology monitoring of small petrel species could be further investigated, but study burrows are likely to be the most advantageous method. The disadvantage of RFID readers is that they do not show directionality and thus limit data analysis. Furthermore, the weekly battery changes are labour-intensive and not ideal for long-term monitoring on remote islands. These shortcomings can be overcome by using paired antennas to assess movement directionality and by using solar panels to power RFID readers (Taylor et al. 2012). However, further study of the SGDP with study burrows may provide the most valuable insights. Neither RFID readers nor remote cameras provide data on feeding portions and chick growth rates, for both methods are limited to assessing activity at the burrow entrance. Consequently, the placement of study burrows should be considered to study the breeding biology of the SGDP more in-depth. This technique may be labour intensive, invasive and potentially limited to a selected suit of SGDP burrows in the most stable soils, but this technique will likely provide the most useful breeding biology data. Considering the precarious state of the SGDP in New Zealand, further breeding biology studies appear favourable, especially since certain
conservation management strategies require detailed breeding biology data (Miskelly & Taylor 2004).

CONCLUSION

Remote cameras provide opportunities to assess interspecific interactions at seabird burrows. However, remote cameras may not be the most feasible method to study the breeding biology of small, burrowing seabirds, especially when these breed in dunes like the South Georgian Diving Petrel on Codfish Island. For in-depth breeding biology studies RFID readers with paired antennas may be considered, but study burrows will likely provide the most detailed data on the South Georgian Diving Petrel in particular and small, burrowing seabirds in general. Chapter 5

Chapter 5. ANALYSIS OF PHENOTYPIC DIFFERENTIATIONS BETWEEN SOUTH GEORGIAN DIVING PETREL (*Pelecanoides georgicus*) POPULATIONS REVEALS AN UNDESCRIBED AND HIGHLY ENDANGERED SPECIES FROM NEW ZEALAND

ABSTRACT

NRESOLVED TAXONOMY OF threatened species is problematic for conservation as the field relies on species as single, distinct, ecological units. New Zealand supports a highly diverse seabird community and their taxonomy is far from resolved. Differences in breeding habitat and results from a preliminary molecular analysis indicated the New Zealand population of the South Georgian Diving Petrel (Pelecanoides georgicus) to be a distinct yet undescribed taxon. I measured 10 biometric characters and scored eight plumage characters in 80 live birds and 53 study skins originating from the majority of the known populations of *P. georgicus*. I analysed differences with factorial ANOVAs, Kruskal-Wallis rank sum tests, and principal component analyses (PCA). Furthermore, I used a species delimitation test with quantitative phenotypic criteria to address species limits within *P. georgicus*. Results show that the New Zealand population differs from other populations through: 1) longer wings, 2) longer outer tail feathers, 3) higher bills, 4) longer heads, 5) longer tarsi, 6) limited collar extent, 7) greater extent of contrasting scapulars and, 8) larger contrasting markings on the secondaries. These differences may be linked to different ecological or behavioural traits. The species delimitation test revealed that the New Zealand population merits species status. I hereby propose to name this new species *Pelecanoides taylorii sp. nov.* Due to severe historic range restrictions and very low number of remaining individuals (approx. 150 individuals limited to Codfish Island (Whenua Hou)) the species warrants listing as Critically Endangered.

INTRODUCTION

Conservation biology remains focussed on species as distinct and single ecological units and thus, accurate taxonomic placement of threatened species is crucial to effective conservation management (May 1990, Sangster *et al.* 2016). If common, polytypic taxa (i.e., clusters of distinct and diverged species; Griffiths 1974), include unclassified taxonomic units warranting species status, their significance remains "hidden". Valuable time to implement conservation management may consequently be lost if composite "species" ameliorate the actual conservation status of threatened taxa (Sangster *et al.* 2016). Therefore, the "hidden" rare taxa are unlikely to receive the management required to conserve them.

This phenomenon of "hidden" but endangered taxa is common on archipelagos and many distinct and endemic taxa on (single) islands are consequently underappreciated (Sangster *et al.* 2016). For instance, the taxonomy of many species complexes on the archipelago of New Zealand remains unresolved (e.g., May 1990, Bell *et al.* 1998, Hay *et al.* 2010). Especially New Zealand's diverse seabird community, the most threatened seabird community in the world (Croxall *et al.* 2012), remains in taxonomic flux (e.g., Penhallurick & Wink 2004, Rheindt & Austin 2005, Rawlence *et al.* 2016, Wood *et al.* 2016) and several undescribed and threatened seabird taxa may remain within polytypic seabird "species" in New Zealand.

The South Georgian Diving Petrel (*Pelecanoides georgicus*; Murphy & Harper 1916) is an example of a potentially polytypic seabird taxon that is currently considered monotypic (Gill *et al.* 2010), but may include a highly threatened and distinct taxon (Paterson *et al.* 2000). This Procellariiform species occurs across the southern hemisphere with breeding colonies on South Georgia (U.K.), Prince Edward Island (South Africa), Crozet Islands (France), Kerguelen Islands (France), Heard Island (Australia) and Codfish Island (Whenua Hou) (New Zealand) (Marchant & Higgins 1990, Figure 11). Other additional colonies were extirpated including colonies on Marion Island (South Africa), Macquarie Island (Australia), Auckland Islands (New Zealand), Chatham Islands (New Zealand), Stewart Island (New Zealand), and the South Island of New Zealand (Marchant & Higgins 1990, Taylor 2000, Wood & Briden 2008). Ecological, molecular and osteological data highlight the possibility that the New Zealand *P. georgicus* population may be a distinct species. For

example, *P. georgicus* in New Zealand prefer coastal sand dunes at sea level for breeding (Taylor 2000, Chapter 3), rather than scree at high altitude as other populations do (Payne & Prince 1979, Marchant & Higgins 1990). In addition, results of a preliminary molecular analysis suggest that the New Zealand population diverged from *P. georgicus* populations in the Southern Indian Ocean several 100,000 years ago, and is indeed distinct (Paterson *et al.* 2000). Furthermore, osteological analyses revealed differences between P. georgicus populations (Worthy 1998). The debate surrounding the taxonomic status of *P. georgicus* in New Zealand has resulted in considerable confusion in the literature (Scofield & Stephenson 2013). While *P. georgicus* is considered of Least Concern globally (IUCN 2016), the New Zealand population is highly threatened (Taylor 2000) and is currently classified as Nationally Critical (Robertson *et al.* 2013).

In order to resolve the taxonomic status of the threatened relict population of *P. georgicus* population in New Zealand, I assessed differences in 10 biometric and eight plumage characters and addressed species limits within *P. georgicus* using a species delimitation test with quantitative phenotypic criteria (Tobias *et al.* 2010).

METHODS

Taxonomy

I adhere here to the taxonomy of Gill *et al.* (2010) in which *P. georgicus* is considered monotypic and a member of the Pelecanoididae family (order: Procellariiformes).

Origin of samples

I assessed biometric and plumage differences between *P. georgicus* populations using 80 live birds and 53 study skins, covering the majority of the range of the species (Marchant & Higgins 1990; Figure 11). I measured and photographed live birds on Codfish Island, New Zealand (n = 64). Furthermore, I used measurements from live birds from Ile aux Cochons, Kerguelen Islands (n = 16) (Bost, Fromant & Miskelly unpub. data 2015). In addition, I measured and photographed study skins deposited in Te Papa Tongarewa Museum of New Zealand, Wellington (NMNZ). NMNZ study skins originated from: South Georgia (n = 4), Marion Island (n = 1), Crozet Islands (n = 4)= 3), Kerguelen Islands (n = 12), Heard Island (n = 10), Codfish Island (n = 10) and Dundas, Auckland Islands (n = 1). To increase my sample sizes, I requested further data and photographs from study skins from the American Museum of Natural History, New York, U.S.A. (AMNH) and the British Museum of Natural History, Tring, U.K. (BMNH). AMNH study skins originated from South Georgia (n = 5). BMNH study skins originated from South Georgia (n = 3), Marion Island (n = 1), Crozet Islands (n = 2) and Auckland Islands (n = 1). Six study skins at BMNH (11.6.1861, 01.9.1861, 1949.51.7, 1938.12.19.102, 1940.12.7.45 and 1991.25.1) were originally labelled as Common Diving Petrel (*P. urinatrix exsul/coppingeri*). I concluded that these skins were in fact *P. georgicus* based on bill morphology (e.g., convergent bill sides and pointed arch; Onley & Scofield 2007) and included samples in my analysis. In total, my sample size included 80 live birds and 53 study skins.





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Biometric characters

I compared 10 biometric variables between populations. Nine different biometric variables were measured (Table 11). In addition, I used the difference between T1 and T6 to enable quantitative assessment of tail fork depth. Measurements were rounded to the nearest mm for wing and tail measurements and to the nearest 0.1 mm for all other measurements. Where applicable, measurements were taken on the right side of the bird. Measurements originated from several different researchers and to counter a potential measuring bias, a short video illustrating the precise measuring methodology was provided (https://youtu.be/gyJnRYW0NKY).

Plumage characters

I created a semi-standardised photo archive of live *P. georgicus* and study skins and assessed five ordinal plumage characters: contrasting ear-covert extent (1-4; Figure 12A), collar extent (1-4; Figure 12B), contrasting white scapular extent (1-4; Figure 12C), shape of white markings on all secondaries (1-4; Figure 13) and extent of white markings on all secondaries (S1-S10) (1-5; Figure 13). In addition, I recorded the colour of the contrasting ear coverts, collar, and flank on a scale (1-5; 1 = white, 5 = black). I refrained from using a colour chart, as this tool is not helpful with colours fading into each other (Collar & Marsden 2014). In several taxonomic studies plumage characters are scored on larger scales (e.g., 1-10; Alström *et al.* 2015, 2016). I refrained from using such scales as they come with the arguable difficulty of distinguishing between neighbouring classes.

Table 9. Definitions and measuring tools of biometric variables used in data collection for analyses of biometric differentiations between *Pelecanoides georgicus* populations.

Biometric	Measuring	Definition
variable	tool	
Wing length	Wing ruler	Flattened wing chord from carpal joint to longest
		primary.
Length of T6	Tail ruler	Distance from point of insertion to tip of the outermost
		tail feather (T6).
Length of T1	Tail ruler	Distance from point of insertion to tip of the innermost
		tail feather (T1).
Bill length	Dial/vernier	Distance on a horizontal plane from front curve of
	callipers	upper mandible to distalmost crown feathers.
Bill width	Dial/vernier	Width at distalmost crown feathers.
	callipers	
Bill height	Dial/vernier	Height (depth) of both mandibles at the distalmost
	callipers	crown feathers, including nostrils (nasal tubes).
Arch length	Dial/vernier	Distance from the apex of the lower mandible arch to
	callipers	the distalmost throat feathers.
Head length	Dial/vernier	Distance from the front curve of upper mandible to the
	callipers	supraoccipital.
Tarsus length	Dial/vernier	Distance from the notch between the digits and the
	callipers	tarsometatarsus to the notch between the
		tarsometatarsus and the tibia.



Figure 12. Scale of variation in plumage characters of *Pelecanoides georgicus* used to assess plumage scores. 11A: extent of contrasting ear coverts (1 = absent, 4 = reaching over the eye). 11B: Extent of collar (1 = absent, 4 = fully connected). 11C: Extent of contrasting scapulars (1 = absent, 4 = prominent and virtually connected).



Figure 13. Matrix used to score variation in the shape of contrasting markings (horizontal; 1 = absent, 4 = present on tip, inner and outer vane) and extent of contrasting markings (vertical; 1 = absent, 5 = covering at least one vane entirely) on all secondaries in different *Pelecanoides georgicus* populations.

Data analysis

I pooled samples of *P. georgicus* into three allopatric populations: South Atlantic Ocean (SAO; n = 12), South Indian Ocean (SIO; n = 45) and South Pacific Ocean (SPO; n = 76 (Onley & Scofield 2007) (Figure 11). I then compared biometric measurements and plumage scores between these pools. I excluded all juvenile birds (SAO = 0, SIO = 8, SPO = 3) from the analyses to account for potential biases created by incomplete feather growth/development. I also excluded T6 and T1 measurements from birds showing active tail moult (SAO = 0, SIO = 5, SPO = 4). Furthermore, I accounted for potential differences between live birds and study skins (e.g., through shrinkage or fading; Kinsky & Harper 1968, Harris 1980) by using Welch's twosample t-tests with the SPO pool as a subset (as this pool had the largest sample size). Based on results from this analysis, I excluded measurements of wing length (t =2.161, df = 15.026, p = 0.047) and bill height (t = -6.149, df = 14.044, p < 0.001) as well as plumage scores of the extent of contrasting ear-coverts (t = -3.371, df = 12.242, p =0.005) and collar colour (t = 2.197, df = 13.437, p = 0.046) from live birds from subsequent analyses. As few samples were sexed, sexual dimorphism was not taken into account. I then assessed differences in biometric measurements using factorial ANOVAs and Tukey HSD tests (Collar & Marsden 2014). I assessed differences in plumage characters with Kruskal-Wallis rank sum tests and made pair-wise comparisons with Welch's two-sample t-tests with Bonferroni corrections (Alström et al. 2015, 2016). In addition, I preformed two principal component analyses (PCA): one for biometric measurements and one for plumage scores. Missing values were replaced with the means of each pool, and data were log transformed before executing a PCA (Quinn & Keough 2002).

I addressed the potential species status of the three allopatric populations using a species delimitation test with quantitative phenotypic criteria (Tobias *et al.* 2010), in which biometric, bioacoustic, plumage and behavioural/ecological characters can be scored. Characters with continuous data (e.g., biometric and bioacoustic data) were scored based on Cohen's *d* effect sizes (d = 0.2-2.0 = score of 1, d = 2.0-5.0 = score of 2, d = 5.0-10.0 = score of 3, d > 10.0 = score of 4). Nominal, ordinal and interval data (e.g., plumage and behavioural characters) were scored more subjectively. An "exceptional" character (e.g., a completely different colour in most of the plumage) received a score of 4, a "strong" character (e.g., a contrastingly different

colour in most of the plumage) a score of 3, a "medium" character (e.g., a slightly different colour in a significant part of the plumage) a score of 2, and a "weak" character (e.g., a different shade in part of the plumage) a score of 1. Three plumage, two bioacoustic, two biometric and one behavioural/ecological character can then be summed. If the sum exceeded a score of 7, species status is warranted. Species status could not be achieved by scoring only "weak" characters. As I restricted the analysis differentiations within the *P. georgicus* complex to biometric and plumage characters, I summed three plumage character to address species limits within *P. georgicus*.

All analyses were conducted in Program R (R Development Core Team 2016) using the effsize (Torchiano 2016) package. PCAs were visualised using the ggplot2 (Wickham 2009) and ggfortify (Horikoshi & Tang 2016) packages.

RESULTS

Univariate statistics for 10 biometric measurements and eight plumage scores from each allopatric *P. georgicus* population can be found in Table 12.

Biometric characters

Results of factorial ANOVAs revealed differences in wing length ($f_{2,39} = 7.643$, p = 0.002), T6 length ($f_{2,92} = 16.154$, p < 0.001), T1 length ($f_{2,87} = 11.986$, p < 0.001), bill height ($f_{2,37} = 11.827$, p < 0.001), head length ($f_{2,112} = 15.994$, p < 0.001) and tarsus length ($f_{2,113} = 15.626$, p < 0.001). Results of pairwise comparisons using Tukey HSD tests revealed two groups within *P. georgicus* that can be readily distinguished: the SAO/SIO group and the SPO group (Table 12 & Figure 14). Results from a PCA showed that there is considerable overlap in biometric measurements between the SAO and SIO, but only limited overlap between the SAO and SPO populations and very little overlap between the SIO and SPO populations (Table 13 & Figure 15A).

Table 10. Mean ± standard error of mean (minimum-maximum; n) and univariate statistics for biometric measurements (in mm) and plumage scores in allopatric *Pelecanoides georgicus* populations (SAO = South Atlantic Ocean, SIO = Southern Indian Ocean, SPO = South Pacific Ocean). Pair-wise comparisons were conducted with Tukey HSD tests for biometric measurements and Welch two-sample t-tests with Bonferroni corrections for plumage scores. Blank indicates *p* > 0.05, * indicates *p* < 0.01 and *** indicates *p* < 0.001.

Character	SAO	SIO	SPO	SAO	SAO	SIO
				vs. SIO	vs. SPO	vs. SPO
Biometric						
measurement						
Wing length	115.75 ± 1.15	116.16 ± 0.84	121.27 ± 0.71			
	(111-124:12)	(109-122: 19)	(117-125:11)		<u>ተ</u>	<u>ተ</u>
Length of T6	38.98 ± 1.15	36.81 ± 0.71	41.07 ± 0.29			ale ale ale
0	(30-45; 12)	(32-40; 13)	(37-48; 69)		*	<u> </u>
Length of T1	35.61 ± 0.70	33.90 ± 0.57	37.40 ± 0.32			***
0	(31-39; 12)	(31-37; 13)	(34-47;65)			ተተተ
Tail fork depth	3.37 ± 1.24	2.66 ± 0.36	3.72 ± 0.24			
I	(-4-11; 12)	(0-5; 13)	(0-10; 65)			
Bill length	14.09 ± 0.27	14.10 ± 0.26	14.08 ± 0.14			
0	(12.3-15.8; 12)	(11.4-17.4; 35)	(11.0-17.4; 69)			
Bill width	8.78 ± 0.36	8.42 ± 0.08	8.56 ± 0.05			
	(6.7-11.3; 12)	(7.6-9.5; 35)	(7.8-10.0; 69)			
Bill height	7.50 ± 0.12	7.74 ± 0.16	8.71 ± 0.20		ماد ماد ماد	ale ale ale
	(6.9-8.2:11)	(6.7-9.5: 19)	(7.8-9.4;10)		<u> </u>	<u> </u>
Arch length	5.80 ± 0.24	5.24 ± 0.15	5.55 ± 0.22			
	(5.0-6.9:7)	(3.8-6.2: 18)	(4.3-6.5; 10)			
Head length	49.49 ± 0.62	49.33 ± 0.52	51.73 ± 0.19		ماد ماد ماد	ale ale ale
	(46.4-53.4:11)	(36.7-56.5: 35)	(45.1-55.5: 69)		<u> </u>	<u> </u>
Tarsus length	23.63 ± 0.84	24.36 ± 0.18	25.60 ± 0.14		ماد ماد ماد	ale ale ale
raioao iongui	(19.3-27.2:12)	(22.0-26.1: 35)	(22.9-28.6: 69)		***	***
Plumage score	(, ,)	(, , , , , , , , , , , , , , , , , , ,				
Contrasting ear	3 42 + 0 19	3 19 + 0 15	3 18 + 0 18			
covert extent (1-4)	(2-4.12)	$(2-4\cdot 21)$	(2-4.11)			
	258 ± 0.22	348 ± 0.18	169 + 0.08			
Collar extent (1-4)	(2-4: 12)	(2-4: 21)	(1-3:58)	**	**	***
Contrasting	(= -, -=)	(= -) = -)	(1 0,00)			
scanular extent (1-	2.33 ± 0.23	2.00 ± 0.16	3.16 ± 0.09		**	***
4)	(1-4; 12)	(1-4; 21)	(2-4; 62)			
Contrasting						
secondary marking	2.17 ± 11	2.00 ± 0.10	3.11 ±0.10		***	***
extent (1-5)	(2-3; 12)	(1-3; 21)	(2-5; 62)			
Contrasting						
secondary marking	3.08 ± 0.15	3.75 ± 0.16	4.00 ± 0.00	**	***	
shape (1-4)	(2-4; 12)	(1-4; 20)	(4-4; 62)			
Contrasting ear	3.08 ± 0.19	3.24 ± 0.10	2.65 ± 0.06			ماد ماد بلہ
covert colour (1-5)	(2-4:12)	(3-4:21)	(2-4:63)			<u> </u>
2 N N (1 = 5)	2.75 ± 0.13	3.00 ± 0.00	2.45 ± 0.28			
Collar colour (1-5)	(2-3:12)	(3-3: 21)	(1-3:11)			
	1.83 ± 0.31	2.50 ± 0.12	1.92 ± 0.08			-la -ll -
Flank colour (1-5)	(2-3; 6)	(2-3; 18)	(1-3; 52)			***



height/depth (SPO having the highest/deepest), collar extent (SIO having the largest), extent of contrasting scapulars (SPO having the NMNZ.18421; origin: South Georgia, U.K., South Atlantic Ocean. SIO = NMNZ.24768; origin: Heard Island, Australia, Southern Indian Figure 14. Dorsal (A), ventral (B), and lateral (C) views of study skins of *Pelecanoides georgicus* from different populations. SA0 = Ocean. C: NMNZ.21631; origin: Dundas Island, Auckland Islands, New Zealand, South Pacific Ocean. Note differences in bill largest), and contrasting white markings on secondaries (SPO having the largest) among others.

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phenotypic characters of several allopatric populations of *Pelecanoides georgicus* (SAO = South Atlantic Ocean, SIO = Southern Indian Figure 15. Principal component analyses for biometric measurements (A) and plumage scores (B) showing the distribution of Ocean, SPO = South Pacific Ocean). **Table 11.** Principal component analysis (PCA) loadings on PC1 and PC2 axes forbiometric measurements in allopatric *Pelecanoides georgicus* populations (Figure15A).

Variable	PC1	PC2
Wing length	-0.450	0.128
Length of T6	-0.423	-0.285
Length of T1	-0.396	0.110
Tail fork depth	-0.140	-0.508
Bill length	-0.065	0.452
Bill width	-0.106	-0.516
Bill height	-0.437	0.037
Arch length	-0.195	-0.069
Head length	-0.301	0.211
Tarsus length	-0.327	0.332

Table 12. Principal component analysis (PCA) loadings on PC1 and PC2 axes forplumage scores in allopatric *Pelecanoides georgicus* populations (Figure 15B).

Variable	PC1	PC2
Contrasting ear covert extent	0.195	-0.608
Collar extent	0.462	-0.110
Contrasting scapular extent	-0.379	-0.328
Contrasting secondary marking extent	-0.425	-0.182
Contrasting secondary marking shape	-0.256	0.287
Contrasting ear covert colour	0.337	0.174
Collar colour	0.410	-0.364
Flank colour	0.275	0.481

Plumage characters

Results of Kruskal-Wallis rank sum tests revealed differences in collar extent (χ^{2}_{2} = 43.685, *p* < 0.001), extent of contrasting scapulars (χ^{2}_{2} = 30.993, *p* < 0.001), extent of secondary markings (χ^{2}_{2} = 41.157, *p* < 0.001), shape of secondary markings (χ^{2}_{2} = 56.870, *p* < 0.001), ear-covert colour (χ^{2}_{2} = 18.400, *p* < 0.001), collar colour (χ^{2}_{2} = 11.223, *p* = 0.004) and flank colour (χ^{2}_{2} = 12.094, *p* = 0.002). Results of pairwise comparisons with Welch's two-sample t-tests with Bonferroni corrections showed that all three pools can be readily distinguished from each other (Table 12 & Figure 14). Results from a PCA revealed that there is limited overlap between the SAO population and the SIO population as well as between the SAO population and the SPO population and very limited overlap between the SIO population and the SPO population (Table 14 & Figure 15B).

Phenotypic species delimitation test

The SAO population differed from the SIO population only in plumage characters: collar extent (reasonably prominent in SAO, while extensive in SIO; score = 2) and the shape of contrasting secondary markings (present on both inner and outer vane in SIO and limited to inner vane in SAO; score = 1). The SPO population differed from the SAO population through: longer wings (d = 1.380; score = 1), a longer T6 (d = 0.771; score = 1), deeper bills (d = 2.324; score = 2), longer heads (d = 1.340; score = 1) and longer tarsi (d = 1.289; score = 1). Plumage scores when comparing the SPO population to the SAO population were the following: collar extent (very limited in SPO, while reasonably prominent in SAO; score = 2), contrasting scapulars extent (very prominent in SPO, while limited in SAO; score = 2), contrasting secondary marking extent (large and prominent in SPO, while limited in SAO; score = 1), shape of contrasting secondary markings (present on both inner and outer vane in SPO and limited to inner vane in SAO; score = 1). The SPO population differed from the SIO population through: longer wings (d = 1.566; score = 1), a longer T6 (d = 1.756; score = 1) and T1 (d = 1.391; score = 1), deeper bills (d = 1.453; score = 1), longer heads (d= 1.087; score = 1) and longer tarsi (d = 1.099; score = 1). Plumage scores when comparing SPO to SIO were the following: collar extent (very limited in SPO, while extensive in SIO; score = 3), contrasting scapulars extent (very prominent in SPO, while limited in SIO, score = 2), contrasting secondary marking extent (large and

prominent in SPO, while limited in SIO; score = 1), ear covert colour (light grey in SPO, while grey in SIO; score = 1) and flank colour (light grey in SPO, while grey in SIO; score = 1). In addition, one behavioural/ecological character was scored. The SPO population specialises in breeding in foredunes at sea level (Chapter 3), while the SIO and SAO populations breeds in scree and scoria at high altitudes (Payne & Prince 1979, Marchant & Higgins 1990; score = 1). When summing the scores of the phenotypic species delimitation test, the SAO and the SIO population both scored a maximum of 3, while the SPO population scored a maximum of 9.

DISCUSSION

The SPO *P. georgicus* population is distinct from both the SAO and SIO populations and exhibits both biometric and plumage characters that are (at least in combination) diagnostic. The SAO population is very similar to the SIO population with only limited differentiation in plumage characters. Results of the quantitative phenotypic species delimitation test showed that the SPO population warrants species status (Tobias *et al.* 2010). Neither the SAO nor the SIO populations merit species status.

Despite providing evidence for the distinctiveness of the SPO *P. georgicus* population, this analysis of differences between *P. georgicus* populations is not exhaustive yet. I have not included bioacoustics, nor osteological characters, nor moulting strategies in my analysis. Results of a preliminary bioacoustic analysis indicate considerable differences, at least between the SIO and SPO populations (calls from birds from South Georgia and the Crozet Islands are audibly coarser than calls from birds from Codfish Island; Payne & Prince 1979, Fischer unpub. data). An extensive bioacoustic analysis may provide further insights on the differentiation of the SPO population and differences between the SIO and SAO populations. Furthermore, an analysis of moulting strategies between the three populations could be informative, for different moulting strategies can also provide clues on the species status of cryptic taxa (Robb *et al.* 2008).

My results indicate that *P. georgicus* from the SPO is a distinct species, but biometric and plumage characters overlap between *P. georgicus* populations. All species within *Pelecanoides* are very similar in both biometrics and plumage

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(Bretagnolle 1993, Onley & Scofield 2007) and thus, the documented amount of overlap in biometric and plumage characters was to be expected.

An assessment of the specimens from Macquarie Island would be most valuable. Mathews hypothesised in 1935 that an undescribed taxon was present on Macquarie Island and proposed to name it *P. georgicus novus* (Gill *et al.* 2010). The extinct Macquarie Island colony (Marchant & Higgins 1990) was likely an easternmost outlier of the SIO population, as Macquarie Island is devoid of sand dunes. On the other hand, the Macquarie Island colony may have been a westernmost outlier of the SPO population. Alternatively, Macquarie Island hosted yet another undescribed taxon within the *P. georgicus* complex.

Even though several species have been described based on solely phenotypic characters (e.g., van Balen *et al.* 2011, Sangster *et al.* 2013, Eaton & Collar 2015, Sangster *et al.* 2016), a thorough molecular analysis of *P. georgicus* would provide useful insights. Such an analysis would provide further information on the status of the SIO and SAO populations and would also complement the preliminary results by Paterson *et al.* (2000). Moreover, I suggest such investigations to extend beyond the *P. georgicus* complex and include the Common Diving Petrel (*P. urinatrix*) complex or even all *Pelecanoides* species.

Despite the various shortcomings of the analysis presented here, the SPO population warrants species status based on the criteria of diagnosability and degree of differentiation. Diagnosability was the most frequently applied species criterion in a review of species criteria in avian taxonomy studies (Sangster 2014). The SPO population of *P. georgicus* exhibits eight phenotypic characters that are, at least in combination, diagnostic. The second most commonly applied criterion was the degree of differences (Sangster 2014). The results of the phenotypic species delimitation test (Tobias *et al.* 2010) suggest that the SPO population of *P. georgicus* differs too much from other populations to be treated as subspecies. Other criteria frequently applied in avian taxonomic studies include different adaptive zones and monophyly (Sangster *et al.* 2014). The SPO populations may qualify as a distinct species under these criteria as well. Differences in breeding habitat may indicate that the SPO population occupies a niche different to the other *P. georgicus* populations (Marchant & Higgins 1990, Chapter 3). In addition, the preliminary molecular analysis by Paterson *et al.* (2000) illustrated that the SPO population has been separated from other *P. georgicus*

populations for several 100,000 years. Given the common use of diagnosability and degree of difference as species criterion (Sangster 2014) and the recent broad and international coverage of the applied phenotypic species delimitation test (Tobias *et al.* 2014) in assessing species limits (del Hoyo *et al.* 2014, IUCN 2016), I conclude that the SPO *P. georgicus* population merits species status. I propose to name this species: *Pelecanoides taylorii sp. nov.*

It should be noted that the following species description should not be seen as a finalised formal description, but as an exercise in taxonomy, part of this thesis.

Diagnosis

P. taylorii differs from both *P. georgicus* populations in the SAO and SIO through: 1) longer wings, 2) longer outermost tail feathers, 3) longer heads, 4) longer tarsi and 5) higher (deeper) bills. In addition, *P. taylorii* differs from the SIO *P. georgicus* population in having longer innermost tail feathers (Table 12 & Figure 14).

The biometric differentiation of *P. taylorii* may be indicative of different ecological or behavioural traits of this taxon. For example, wing length is often related to travel distances to and from foraging areas (Shaffer *et al.* 2001) and foraging behaviour (Hertel & Balance 1999). Therefore *P. taylorii* may travel further during breeding seasons or migrate farther non-breeding seasons than the SAO and SIO populations of *P. georgicus*. In addition, bill morphology is often adapted to feeding ecology (Imber 1981). The different bill height of *P. taylorii* may be linked to different foraging strategies or prey species. Furthermore, tarsus length may be related to burrowing behaviour, as diving petrels (*Pelecanoides* ssp.) dig their burrows using their legs. *P. taylorii* on Codfish Island have comparatively long burrows ($\bar{x} = 0.8$ m; Marchant & Higgins 1990). Alternatively, tarsus length may be related to swimming behaviour (Marchant & Higgins 1990).

P. taylorii differs from *P. georgicus* of both SAO and SIO populations through several well developed and more contrasting plumage characters: 1) the very limited collar that is only visible on the breast sides, 2) well defined and prominent, contrasting white scapulars and, 3) large contrasting white markings on secondaries.

In addition, *P. taylorii* differs from the SAO *P. georgicus* through contrasting markings on both inner and outer vanes of the secondaries. Furthermore, *P. taylorii* differs from SIO *P. georgicus* through lighter grey ear coverts and flanks (Table 12 Figure 14).

The different plumage traits of *P. taylorii* may be indicative of different life history traits. Procellariiformes with paler plumages forage in colder waters at higher latitudes (Bretagnolle 1993). Therefore, it is likely that the contrasting, pale plumage characters, diagnostic of *P. taylorii*, have developed due to more southerly foraging areas than *P. georgicus*. Furthermore, plumage colouration may also be related to high inshore predation pressure, which potentially drives crypsis in small Procellariiformes (Bretagnolle 1993). The more conspicuous *P. taylorii* may thus feed further off shore than the duller *P. georgicus*.

Generic placement

P. taylorii clearly belongs in *Pelecanoides*, Lacepédè 1799, (family: Pelecanoididae, order: Procellariiformes) rather than any other genus within Procellariiformes based on a combination of short, paddle-like wings, short tail, small and compact build and bill morphology (short, broad based bill with hooked tip and throat pouch) (Onley & Scofield 2007, Gill *et al.* 2010).

Etymology

The scientific name honours GA Taylor, one of New Zealand's leading seabird scientist, who dedicates his life to the preservation of New Zealand's seabird diversity (e.g., Taylor 2000) and is actively involved in the conservation of the New Zealand Storm Petrel (*Paeleornis maoriana*; e.g., Rayner *et al.* 2015), Chatham Petrel (*Pteroroma axillaris*; e.g., Gummer *et al.* 2015), Chatham Island Taiko (*Pterodroma magentae*; e.g., Taylor *et al.* 2012) and *P. taylorii* (e.g., Taylor & Cole 2002, Taylor 2013) among many others. I propose the following common species name: Dunehaunter. This name refers to the distinct preference exhibited by this species for breeding in coastal dune systems, as well as the nocturnal habits of the species.

Holotype

NMNZ.21631 (adult female), collected at Dundas Island, Auckland Islands, New Zealand, on 28 October 1943 by RA Falla (Figure 14). Previously assigned to *P. georgicus*.

Paratypes

The following 11 specimens were all previously assigned to *P. georgicus* and used in the species description of *P. taylorii*: BMNH.1842.12.16.41 (sex and age unknown), collected at Enderby Island, Auckland Islands, New Zealand, by RA Falla. NMNZ.21057 (adult male) and NMNZ.21058 (adult female), both collected at Codfish Island, New Zealand, on 22 September 1978 by MJ Imber. NMNZ.21070 (female) and NMNZ.21071 (adult female), both collected at Codfish Island, New Zealand, on 17 November 1978 by PC Harper. NMNZ.27537 (adult male), NMNZ.27538 (adult male), NMNZ.27539 (adult female), NMNZ.27540 (adult female) and NMNZ.27541 (adult male), all collected at Codfish Island, New Zealand, in September/October 2003 by the New Zealand Department of Conservation (DOC).

Description of the holotype

HEAD: the forehead and crown are glossy black. The nape is glossy black, but feather bases are light grey. The lores are black. The cheeks and ear coverts are mottled and light grey, creating a prominent and contrasting pattern. A small dark grey patch above the eye gives the appearance of a restricted brow/supercilium (Figure 14AC).

UPPERPARTS: The mantle feathers have light grey bases and glossy black tips. The scapulars are pure white, prominent, contrasting and almost connected above the rump. The rump and back are glossy black, but feather bases are white. The uppertail coverts have broad white bases and glossy black tips (Figure 14A).

UNDERPARTS: The chin, throat and upper breast are dirty white, while the lower breast, belly and undertail coverts are pure white. The breast and neck sides are mottled light grey, resulting in a small collar. The flanks are smudged light grey (Figure 14B).

WING: The upperwing coverts (both primary and secondary) and tertails are glossy black with a brown hue and glossy black tips. Dorsally, the primaries are dull black with a brown hue. Ventrally, the primaries have dirty white inner vanes and light grey outer vanes. The third outermost primaries are the longest. The secondaries are dull black on the outer vane dorsally and dark grey ventrally, while the inner vane is light grey (both dorsally and ventrally). The secondaries have broad white tips extending towards the base on both inner and outer vanes. The secondary feather tips are fringed outwards. The underwing coverts (both primary and secondary) are pure white, while the axillaries are light grey (Figure 14 AC).

TAIL: The retrices are dull black dorsally and dark grey ventrally, apart from the outermost pair, which is light grey on the inner vane. The two outer retrices (T6 & T5) are longer than the inner retrices (T4-T1; T1 being the shortest), resulting in a shallow tail fork (Figure 14A).

BARE PARTS: the bill is black, with a hooked tip, a broad base and convergent bill sides. The lower mandible arch is pointed and sides are dull brown, suggesting a faded colour (live birds have sky blue lower mandible arch sides). The nostrils (nasal tubes) are black, parallel and facing upwards with a medial paraseptal process. The gular pouch is dark grey. The legs and webbed feet are dull brown, suggesting a faded colour (live birds have cobalt blue legs), with a hint of a black line on the back of the tarsus. The claws are black and flattened.

Variation in type series

NMNZ.21058 (adult female) differs from holotype through: 1) a black brow, and 2) grey outer retrices. NMNZ.21070 (female) differs from holotype through: 1) a black brow, 2) black cheeks, 3) grey ear coverts, 4) small contrasting ear patch extent, and 5) small extent of contrasting white scapulars. NMNZ.21071 (adult female) differs from holotype through: 1) a black brow, 2) grey ear coverts, and 3) a more prominent collar. NMNZ.27539 (adult female) differs from holotype through: 1) grey ear coverts, 2) black cheeks, and 3) pure white flanks. NMNZ.27540 (adult female) differs from the holotype through: 1) a black brow, 2) black cheeks, 3) grey ear coverts, 4) grey outer retrices, 5) pure white flanks, and 6) small amount contrasting white markings on secondaries.

NMNZ.21057 (adult male) differs from holotype through: 1) a black brow, and 2) grey ear coverts. NMNZ.27537 (adult male) differs from holotype through: 1) a black brow, 2) black cheeks, 3) grey ear coverts, and 4) a more prominent collar. NMNZ.27538 (adult male) differs from holotype through: 1) pure white flanks, and 2)

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black cheeks. NMNZ.27541 (adult male) differs from holotype through: 1) a black brow, 2) black cheeks, 3) grey ear coverts, 4) a more prominent collar, and 5) grey outer retrices.

BMNH.1842.12.16.41 (sex unknown) differs from holotype through: 1) a black brow, 2) grey ear coverts, and 3) a more extensive grey collar.

Identification at sea

Diving Petrels are notoriously difficult to identify at sea (Onley & Scofield 2007). For example, distinguishing *P. urinatrix* from *P. georgicus* is close to impossible, unless very clear photographs are obtained. Even high resolution photographs are unlikely to clearly depict the subtle differences between *P. georgicus* and *P. taylorii*. As it is currently unknown whether ranges overlap, albeit unlikely, it appears impossible to positively identify *P. taylorii* at sea.

Distribution

All known specimens of *P. taylorii* originate from either Dundas Island, Enderby Island (Auckland islands, New Zealand), or Codfish Island, New Zealand (Figure 1). *P. taylorii* remains extant only on Codfish Island only, where it breeds in a minute (20 x 900 m) strip of coastal sand dunes in the Sealers Bay (Chapter 3 & 4). The historic distribution of *P. taylorii* in New Zealand encompassed the Otago Peninsula on the South Island, Mason's Bay on Stewart Island, Enderby and Dundas Islands on the Auckland Islands and Chatham Islands (Worthy 1998, Taylor 2000, Holdaway *et al.* 2003, Wood & Briden 2008). The historic presence of *P. taylorii* on Macquarie Island remains uncertain. The offshore distribution of *P. taylorii* also remains unknown. Some evidence indicates that the species forages on the edge of the continental shelf during the breeding season (Imber & Nilsson 1980). Future studies investigating offshore distribution during breeding and non-breeding season of *P. taylorii* (and *P. georgicus* from the SAO and SIO populations) are encouraged.

Habitat & biology

P. taylorii breeds in long burrows in coastal sand dunes. It prefers foredunes (0-20 meter from spring tide line) with steep, seaward-facing slopes, high sand flux and 50-80% plant cover (Chapter 3). *P. taylorii* appears to be tolerant to the current suite of

invasive plants at Codfish Island. *P. taylorii* presumably returns to Codfish Island from its unknown wintering grounds in October (Taylor 2013). Eggs hatch in late November. Chicks fledge in mid to late January (Taylor 2013, Fischer unpub. data). Nocturnal change-over rates of adults are approximately four days during incubation and one day during chick rearing (Taylor & Cole 2002, Taylor 2013, Fischer unpub. data). Information on prey items remains equally anecdotal, with two specimens having eusphausiids, small fish and small squids in their stomachs (Imber & Nilsson 1980).

Conservation implications

P. georgicus is currently considered Least Concern by the IUCN (2016). The proposed split of *P. georgicus* would not change the conservation status for the SAO and SIO *P. georgicus* populations. Both still number in the millions, both have a large range, and there are no indications of any current population declines (Marchant & Higgins 1990, Brooke 2004).

However, P. taylorii is at extremely high risk of extinction. The range of P. taylorii has decreased dramatically in the past and the species has been extirpated throughout its range, most likely due to introduced predators (Worthy 1998, Taylor 2000, Holdaway et al. 2003, Wood & Briden 2008). P. taylorii is now restricted to Codfish Island and the population size is estimated at 150 adults (Taylor 2013). The DOC therefore, considers this taxon Nationally Critical (Robertson et al. 2013). Therefore, I propose to list *P. taylorii* as Critically Endangered on the IUCN Red List. When applying the IUCN (2012) criteria to *P. taylorii*, it qualifies for listing as Critically Endangered, based on criteria B2ab (ii, iii) and C2a (ii). *P. taylorii* has an extremely limited area of occupancy during the breeding season (20 x 900 m) at only a single location. Its habitat is degrading due to storms and storm surges, which reduce the area of occupancy (Taylor & Cole 2002, Cole 2004, Chapter 3). Furthermore, the estimated population size is very small (approx. 150 adults; Taylor 2013), all individuals are part of this one population and a decline is expected due to the impact of storms and storm surges during breeding seasons (Chapter 3). Moreover, competition with *P. urinatrix* for nest sites may be a minor threat to *P. taylorii* (Chapter 4). Critically Endangered is indicative of an extremely high risk of extinction

(IUCN 2012), and thus underlines the need of conservation prioritization for *P. taylorii*.

CONCLUSION

Here, I provide evidence of the distinctiveness of the Dunehaunter (*Pelecanoides taylorii sp. nov.*; previously part of the South Georgian Diving Petrel *P. georgicus* complex), which is a Critically Endangered taxon. The conservation status of this species has remained "hidden" to global conservation panels due to the inclusion in a polytypic "species". New Zealand maintains a national threat classification system (Robertson *et al.* 2013) and therefore, the dire situation of the *P. taylorii* has been acknowledged within New Zealand. Consequently, national threat classification systems that complement global threat classification systems should be advocated, as they may classify and protect taxa for which the taxonomy is still unclear. In addition, taxonomists are advised to focus on polytypic species that are likely to include threatened taxa (Sangster *et al.* 2016), for conservation efforts depend on species being a clear and single ecological unit.

Chapter 6

Chapter 6. GENERAL CONCLUSION

I N CHAPTER 2, I illustrated that small Procellariiformes in New Zealand are most often threatened onshore by invasive predators, but additional other terrestrial threats exist, which can fall under both the small and the declining population paradigm (Caughley 1994). This predicament is illustrated by the New Zealand population of the South Georgian Diving Petrel (*Pelecanoides georgicus*; SGDP). In Chapter 5, I provided evidence granting this population species status, based on the criteria of diagnosability and degree of difference (Sangster 2014). In Chapter 3, I demonstrated that this potential Codfish Island (Whenua Hou) endemic is under considerable threat from stochastic events, such as storms, causing erosion of the preferred breeding habitat (i.e. fragile foredunes). Moreover, in Chapter 4, I argued that competition for nest-sites with the Common Diving Petrel (*P. urinatrix*; CDP) may form a minor additional risk for this SGDP population.

To effectively address the small population paradigm in the SGDP in New Zealand, a translocation might be considered to conserve this highly-threatened population. This population depends on steep, seaward-facing foredunes with mobile soils for breeding (Chapter 3) and evidence suggests that stochastic events, such as storms and storm surges, will continue to threaten the its colony during the breeding season by eroding these foredunes (Cole 2004, Blair 2007, Hennessy *et al.* 2007). Based on these results, I conclude that environmental stochasticity is the most pressing known threat to this species, which falls under the small population paradigm (Caughley 1994). Yet any investment in storm protection (e.g., a storm wall) is unlikely to result in a population increase, as the distinct preference of this species for fragile foredunes may not change. A translocation however, may render this species less vulnerable to stochastic events and catastrophes, enable SGDPs to recolonize other areas of their historic distribution in New Zealand, and allow the SGDP population to increase. In addition, recolonizing New Zealand's dune systems with SGDPs would reinstate historic dune ecosystem functioning.

Chapter 6

Procellariiformes tend not to recolonize extirpated colonies due to their high philopatry (Miskelly *et al.* 2009). Therefore, translocations are a common tool to restore lost colonies and render Procellariiform species less vulnerable (Miskelly & Taylor 2004, Miskelly *et al.* 2009). However, seabird translocation techniques depend on detailed information on breeding biology and activity, as pre-fledging chicks are used in translocations and thus, techniques need to be tailored to mimic the natural breeding biology of the target species (Miskelly & Taylor 2004, Miskelly *et al.* 2009). Methods developed to translocate CDPs could form a guideline for a SGDP translocation (Miskelly & Taylor 2004). Yet, ideally data from the target species should be used to design translocation strategies. Non-invasive methods used to study the breeding biology and activity patterns of the SGDP on Codfish Island proved to be suboptimal (Chapter 4). Consequently, the placement of study burrows should be considered to study the breeding biology of the species more in-depth and thus provide the data necessary to structure a future translocation.

The population of the SGDP is extremely small (approx. 150 individuals; Taylor 2000, 2013), a translocation of this species has never been attempted and consequently, the development of a species-specific population dynamics model using data from the Codfish Island population is advisable. This would allow for future SGDP translocations to be tested in a theoretical framework. A population modelling approach would enable for a translocation to be planned and structured while minimizing the impact on the source population in the long-term (Armstrong & McLean 1995). It seems advisable to include effects from environmental stochasticity and catastrophes into such models (Armstrong & Reynolds 2012), due to the susceptibility of the species to storms during the breeding season (Chapter 3). Furthermore, the CDP population within the SGDP colony on Codfish Island should be further monitored and its long-term impact on the species quantified (Chapter 4). A competition parameter could then also be included in the population dynamics model to further assess SGDP (and CDP) population trends. Finally, a trial translocation within Codfish Island would allow for assessment of the potential success rate and thus further fine-tuning of the population dynamics model and SGDP translocation techniques. Only after these necessary steps, it seems advisable to attempt a translocation of this species to other islands and thus, mitigate the current risks of the

small population paradigm to the New Zealand population of the South Georgian Diving Petrel on Codfish Island.

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APPENDICES

Appendix 1. References used to construct databases on threats and conservation actions of New Zealand's Procellariiformes (Appendix 2 & 3).

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Appendix 2. Presence/absence matrix of threats faced by New Zealand's Procellariiformes. • = onshore threat present, o = offshore

Appendices

References	2, 91, 92, 95, 97, 118, 122, 138	2, 64, 91, 92, 95 - 97, 118, 122, 124, 138 144	2, 17, 42, 48, 50, 55, 62, 63, 81, 91,	95 - 97, 118, 122, 123, 138 2, 91, 118, 124, 138	31-91.117.118		43, 34, YL, LL8	91, 118	91, 103, 118, 124		43, Y1, Y2, I18	43, 55, 56, 118	3, 45 - 47, 89, 91, 114, 115, 118,	133 17, 79, 91, 118	2 91 96 118 138	CC1 (CT1 (CC (TC (7	2, 91, 96, 97, 118, 124, 138	2, 24, 55, 91, 95, 118, 123, 124, 138	118		1, 2, 64, 65, 91, 92, 95 - 98, 118, 122 - 124 - 138	2, 38, 39, 91, 96, 118, 123, 124, 135, 138
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IS	•	•	•	•	•				•	•	•	•	•	•	•		•	•			•	•
Scientific name	Macronectes halli	Daption	Pterodroma	macroptera Pterodroma	lessonii Pterodroma	magentae	Pteroaroma nealecta	Pterodroma	Pterodroma	inexpectata	Pteroaroma cervicalis	Pterodroma	nigripennis Pterodroma	axillaris Pterodroma	pycrofti Pachvntila	vittata	Pachyptila desolata	Pachyptila	turtur Pachyptila	crassirostris	Procellaria a paninoctialis	Procellaria westlandica
English name	Northern Giant Petrel	Cape Petrel	Great-winged Petrel	White-headed Petrel	Chatham Island	Taiko	kermadec Fetrel	Soft-plumaged Petrel	Mottled Petrel		wnite-napea Petrel	Black-winged Petrel	Chatham Petrel	Pycroft's Petrel	, Broad-hilled Prion		Antarctic Prion	Fairy Prion	Fulmar Prion		White-chinned Petrel	Westland Petrel

English name	Scientific name	IS	NP	HL	HD	ES	ິວ	D.P	LF	NF	RC]	MP	OS	LP	CC	References
Black Petrel	Procellaria narkinsoni	•	•					•	0	0			0			2, 9 - 11, 40, 51, 55, 64, 91, 95 - 97, 118 122 - 124 138
Grey Petrel	Procellaria cinerea	•	•						0	0						2, 8, 64, 91, 92, 95 - 97, 118, 122 - 124 138
Wedge-tailed	Puffinus	•			•	•										43, 91, 118
Shearwater Buller's	pacificus Puffinus bulleri	•			•				0	0	0		0		\bigcirc	2, 55, 91, 92, 95, 118, 124, 138, 144
Shearwater Flesh-footed	Puffinus	•			•	•	•		0	0		0	0			2, 17, 18, 44, 55, 58, 64, 90, 91, 92,
Shearwater Sooty Shearwater	carneipes Puffinus griseus	•		•	•	•	•		0	0				\bigcirc	\bigcirc	95 - 97, 118, 122 - 124, 138 1, 2, 17, 44, 55, 59, 64, 70, 91, 92, 95 00, 105, 106, 110, 123, 123, 120
Fluttering	Puffinus gavia	•			•	•			0	0	0	0	0			- 76, 103, 106, 116, 122 - 124, 136 2, 17, 55, 91, 118, 122, 124, 138, 144
Silear water Hutton's	Puffinus huttoni	•	•		•	•			0	0	0		0	۲		25, 26, 27, 28, 91, 108, 118
Snearwater Little Shearwater Subantarctic Little	Puffinus assimilis Puffinus elegans	•			٠	•	•		0	0						17, 43, 55, 79, 91, 118 118
Shearwater Grey-backed Storm	Garrodia nereis	•	•	•	•	•			0			0		۲		118, 138
White-faced Storm	Pelagodroma marina	•		•	•			•	0	0				۲		2, 55, 91, 118, 123, 124, 138, 145
Kermadec Storm	Pelagodroma	•				•	•			0						43, 49, 91, 118
New Zealand Storm	Pealeornis	•	•													55, 82, 91, 118
Black-bellied Storm	rituor trua Fregetta tropica	•				•			0	0				۲		2, 91, 92, 118, 124, 138
White-bellied Storm Dotrol	Fregetta	•				•										43, 91, 118
Common Diving	grununu Pelecanoides mrinatrix	•	•	•	•	•	•		0	0				۲		2, 17, 55, 91, 95, 96, 116, 118, 122, 124–127–138
South Georgian Diving Petrel	Pelecanoides georgicus	•	•	•	•	•								۲		23, 91, 116, 118, 126, 127

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Appendices

action present, o = offshore conservat Procellariidae, orange = Hydrobatida competition management, HM = habii distribution mapping, DS = diet studie population survey/census, PD = popu al. (2010). References can be found ir al. (2010). References can be found ir Antipodean <u>Diomedea</u> • Antipodean <u>Diomedea</u> • Albatross <u>antipodensis</u> • Albatross <u>anfordi</u> Grey-headed <u>Thalassarche</u> • Albatross <u>Ranfordi</u> Grey-headed <u>Thalassarche</u> • Albatross <u>Ranfordi</u> Grey-headed <u>Thalassarche</u> • Albatross <u>Black-browed Albatross</u> Buller's Albatross <u>Thalassarche</u> • Buller's Albatross <u>Thalassarche</u> •	present, (•) = n a = Pelecanoidi ment, HDM = h catch assessme amics and bree 1. 1 HM HDM	on-spatia dae. IC = uman dis ent, BM b aing biol o T PD	al cons sturba by-cato ogy re ogy re	serval ive sp ince n ch ma ssearc ssearc	tion a becies manager ch. Tay A BN	ction J contra ement, J nent, J Konom		t. Bla = na ranslo ollutio PD	ck = Diomedeidae, blue = tive predator control, CM = ocations, PDM = pelagic on assessment, PS.C = enclature is based on Gill <i>et</i> References
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White-capped <i>Thalassarche</i> Albatross <i>cauta</i>	•	0	0	0	0		۲	۲	1, 2, 7, 30, 64, 91, 92, 94 - 97, 118, 122 - 125, 138
Chatham Island <i>Thalassarche</i> Albatross <i>eremita</i>		•	0	0	0	0	۲	۲	2, 4, 13, 30, 32, 37, 64, 77, 91, 93 - 96, 118, 122, 124, 138
Salvin's Albatross <i>Thalassarche</i> <i>salvini</i>		0	0	0	0		•		2, 6, 30, 64, 68, 91, 92, 94 - 98, 100, 101, 118, 122 - 124, 138

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IC	•		•	•	•	•	•	•		•	٠	•	•	•	•	•	•	•
Scientific	Phoebetria	palpebrata	Macronectes halli	Daption capense	Pterodroma macroptera	Pterodroma lessonii	Pterodroma	muyenue Pterodroma nealecta	Pterodroma	mouus Pterodroma	inexpectata Pterodroma	cervicalis Pterodroma	nigripennis Pterodroma	axillaris Pterodroma	eooku Pterodroma	Pachyptila Viittata	Pachyptila Pachyptila Aocolata	Pachyptila turtur
English name	Light-mantled	Sooty Albatross	Northern Giant Petrel	Cape Petrel	Great-winged Petrel	White-headed Petrel	Chatham Island	t alko Kermadec Petrel	Soft-plumaged	Petrel Mottled Petrel	White-naped	Petrel Black-winged	Petrel Chatham Petrel	Cook's Petrel	Pycroft's Petrel	Broad-billed	Antarctic Prion	Fairy Prion

Appendices

References	30, 64, 118	1, 2, 30, 64, 65, 91, 92, 94 -98, 118 122 - 124 138	2, 30, 38, 60, 64, 91, 94 – 96, 118, 123, 124. 135 - 138. 143	2, 9 - 11, 30, 35, 40, 46, 51, 55, 64, 91, 94 - 97, 118, 122 - 124, 138	2, 8, 30, 64, 91, 92, 94 - 97, 118, 122 - 124, 138	30, 43, 64, 91, 118, 129	2, 30, 55, 64, 91, 94, 95, 118, 124, 138, 144	2, 17, - 19, 30, 44, 55, 58, 64, 90 - 92, 94 - 97, 118, 119, 122 - 124, 138	1, 2, 17, 22, 30, 33, 44, 55, 59, 64, 91, 92, 94, 95 - 98, 106, 107, 118, 119, 122 - 124, 138	2, 12, 17, 19, 30, 46, 55, 64, 69, 91, 94, 95, 104, 118, 119, 122, 124, 138, 144	5, 25 - 28, 30, 64, 69, 91, 94, 108, 118, 119	14, 15, 17, 30, 43, 55, 64, 79, 91, 118, 129	30, 64, 118	2, 30, 64, 118, 138	2, 30, 46, 55, 64, 91, 118, 123, 124, 138, 145	30, 43, 49, 64, 91, 118, 129
PD			٢	۲			۲	۲	۲	۲				۲	۲	
PS.C		۲	۲	۲	۲		۲		۲		۲	۲	۲	۲	۲	•
PA							0	0		0						
BM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BA		0	0	0	0	0	0	0	0	0	0	0		0	0	0
DS		0	0	0	0		0	0	0	0	0	0		0	0	
PDM		0	0	0	0	0	0	0	0	0	0	0			0	0
F				•				•		•	•				•	
MDH			•					•	•							
МН																
CM																
NPC																
IC	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•
Scientific	Pachyptila	er user user is Procellaria aeminortialis	Procellaria westlandica	Procellaria parkinsoni	Procellaria cinerea	Puffinus pacificus	Puffinus bulleri	Puffinus carneipes	Puffinus griseus	Puffinus gavia	Puffinus huttoni	Puffinus assimilis	Puffinus elegans	Garrodia nereis	Pelagodroma marina	Pelagodroma albiclunis
English name	Fulmar Prion	White-chinned	Westland Petrel	Black Petrel	Grey Petrel	Wedge-tailed Shearwater	Buller's Shearwater	Flesh-footed Shearwater	Sooty Shearwater	Fluttering Shearwater	Hutton's Shearwater	Little Shearwater	Subantarctic Little Shearwater	Grey-backed Storm Petrel	White-faced Storm Petrel	Kermadec Storm Petrel

Iname New Zealand Storm Pealeornis • Petrel maorina • • Petrel maorina • • • Black-bellied Storm Fregetta •							
New Zealand StormPealeornis•Petrelmaorina•PetrelFregetta•Petreltropica•White-bellied StormFregetta•Petrelgrallaria•Petrelgrallaria•Common Diving PetrelPelecanoides•urinatrixurinatrix•							
PetrelmaorinaBlack-bellied StormFregettaPetreltropicaWhite-bellied StormFregettaPetrelgrallariaOmmon Diving PetrelPelecanoidesurinatrixo			0	0	•	۲	30, 64, 82, 83, 91, 110, 111 -
Black-bellied Storm Fregetta • 0 0 0 Petrel tropica • • 0 <td></td> <td></td> <td></td> <td></td> <td>)</td> <td>)</td> <td>113</td>))	113
Petrel tropica White-bellied Storm Fregetta Petrel grallaria Common Diving Petrel Pelecanoides		0	0	0	•	•	2, 30, 64, 91, 92, 118, 124, 138
White-bellied Storm Fregetta •))	
Petrel <i>grallaria</i> Common Diving Petrel <i>Pelecanoides</i> • o c urinatrix	0	0	0	0	•	•	30, 43, 64, 91, 118, 129
Common Diving Petrel Pelecanoides • • O C uringtrix))	
urinatrix	•	0	0	0	•		2, 17, 23, 30, 33, 46, 55, 64, 67,
))	69, 91, 96, 116, 118, 119, 122,
							124, 138
South Georgian Diving <i>Pelecanoides</i> • •				0	0		23, 30, 64, 91, 116, 118, 126,
Petrel <i>georgicus</i>))	127, 140

Sand flux																	-0.308***
Aspect																0.152^{*}	-0.078
Slope															0.221^{**}	0.104	-0.269***
Sand	penetrability													-0.433***	-0.305***	-0.111	0.243***
Invasive	ratio												-0.002	-0.176*	0.025	0.237***	-0.359***
Plant	cover											0.021	0.384***	-0.470***	-0.133	-0.361***	0.687***
Distance to	nearest	Puffinus	griseus								0.313^{***}	0.172	0.185^{**}	-0.131	-0.035	0.007	0.281***
Distance to	nearest P.	urinatrix							C C U U	0.022	0.189^{**}	0.009	0.173^{*}	-0.195**	0.0268	0.0869	0.133
Distance to	nearest	conspecific						760.0	0.100**	06110	0.602***	-0.265***	0.454***	-0.382***	-0.341***	-0.326***	0.607***
Distance to	sea					70/0		600.0	000	700.0	0.645***	-0.240***	0.458***	-0.439***	-0.385***	-0.433***	0.612***
				Distance to sea	Distance to nearest	conspecific	Distance to nearest	P. urinatrix	Distance to nearest	Puffinus griseus	Plant cover	Invasive ratio	Sand penetrability	Slope	Aspect	Sand flux	Plant height

Georgian Diving Petrels (*Pelecanoides georgicus*) in the whole dunes. Variables with $r \ge 0.6$ (bold) are considered highly correlated. * Appendix 4. Spearman correlation coefficients (r) between explanatory variables potentially affecting nest-site selection in South indicates p < 0.05, ** indicates p < 0.01 and *** indicates p < 0.001.

Appendix 5. Spearman correlation coefficients (r) between explanatory variables potentially affecting nest-site selection in South
Georgian Diving Petrels (<i>Pelecanoides georgicus</i>) in the foredune. Variables with $r \ge 0.6$ (bold) are considered highly correlated. *
indicates $p < 0.05$, ** indicates $p < 0.01$ and *** indicates $p < 0.001$.

	Distance	Distance to	Distance to	Distance to	Plant	Invasive	Sand	Slope	Aspect	Sand
	to sea	nearest	nearest <i>P</i> .	nearest Puffinus	cover	ratio	penetrability			flux
		conspecific	urinatrix	griseus						
Distance to sea										
Distance to nearest	**C7C U									
conspecific	707.0									
Distance to nearest										
P. urinatrix	0,00	170.0								
Distance to nearest	0 110***	0.00	C F F U							
Puffinus griseus	014'0-	000.0-	71170							
Plant cover	0.170	0.048	0.155	0.283**						
Invasive ratio	0.161	-0.005	0.184^{*}	0.320***	0.506***					
Sand penetrability	0.221*	0.190*	0.164	0.061	0.164	0.234^{*}				
Slope	-0.273**	-0.280**	-0.216**	-0.042	-0.274**	-0.405***	-0.524***			
Aspect	-0.491***	-0.281**	0.113	0.243**	0.075	0.107	-0.279**	0.180		
Sand flux	-0.252**	0.009	0.176	0.210*	-0.130	0.151	0.090	-0.110	0.077	
Plant height	0.053	0.032	0.036	0.158	0.499***	090.0	-0.067	0.013	0.145	-0.064